THE ECOLOGY OF THE LOWLAND TAPIR IN MADRE DE DIOS, PERU: USING NEW TECHNOLOGIES TO STUDY LARGE RAINFOREST MAMMALS

A Dissertation

by

MATHIAS WERNER TOBLER

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2008

Major Subject: Wildlife and Fisheries Sciences

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ABSTRACT

The Ecology of the Lowland Tapir in Madre de Dios, Peru: Using New Technologies to Study Large Rainforest Mammals. (May 2008)

Mathias Werner Tobler, M.S., Swiss Federal Institute of Technology Zürich

Co-Chairs of Advisory Committee: Dr. Rodney L. Honeycutt
Dr. Raghavan Srinivasan

The objectives of my research were twofold: 1) to evaluate new technologies (camera traps and a new type of GPS collar) for studying large mammals in tropical forests, and 2) to study the ecology of the lowland tapir (*Tapirus terrestris*) in the Peruvian Amazon.

Camera traps proved to be an efficient tool for mammal inventories in tropical forests. They recorded 24 out of 28 terrestrial medium and large sized mammal species with a survey effort of 2340 camera days. Camera traps were also able to reveal important information on habitat use, activity patterns and the use of mineral licks for five Amazonian ungulate species. There was a high spatial overlap between all the species with the grey brocket deer being the only species that was restricted to *terra firme* forest. White-lipped peccaries, tapirs and red brocket deer frequently used mineral licks, whereas collared peccaries and grey brocket deer were hardly ever observed at licks.

A new type of GPS collar (TrackTag) tested in this study performed well under the dense canopy of a tropical forest. Position success rates of 87% for stationary collars and 48% for collars placed on tapirs were comparable to data obtained with GPS collars in temperate forests. The mean location error for stationary collars inside the forest was 28.9 m and the 95% error was 76.8 m.

GPS collars placed on six tapirs for seven to 182 days showed home range sizes of 102 to 386 hectares. Tapirs were mainly nocturnal and areas used for foraging during the night differed from resting sites used during the day. Tapirs could walk up to 10 km to visit a mineral lick. Visits were irregular at intervals of a few days up to 36 days.

The analysis of 135 tapir dung samples showed that tapirs ingest seeds of over 120 plant species. Seeds were found throughout the year but monthly species diversity was related to fruit availability. The size distribution of ingested seeds was related to availability. Most seeds were less then 10 mm wide, but seeds up to 25 mm were found.

Both camera traps and TrackTag GPS collars greatly increased the possibilities for studying large rainforest mammals. The two technologies collect complementary information and each one is suited for a different set of questions.

DEDICATION

To Javier Huinga and Dario Cruz Jr. who worked as hard as I did

to make this work possible

and

to my family

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First of all I would like to thank my friend and colleague John Janovec, who first invited me to Peru and who supported my work and led the Andes to Amazon Biodiversity Program (AABP) throughout these years. Without his continuous help and advice, this research would not have been possible. I am also very grateful to Louise Emmons for all the advice she gave me with regard to study design, captures, and logistics and for all the inspiring discussions that led to new questions and ideas for this project.

A special thank you goes to my two field assistants Javier Huinga and Dario Cruz Jr., who during the last three years, worked at my side in the forest catching and tracking tapirs, checking cameras, collecting samples, and teaching me about the forest and the local culture. Their dedication and hard work made this research possible.

I would like to thank all the veterinarians who helped me with the tapir captures, anesthesia protocols, and the health study: Carlos Sanchez, Valeria Moreno, César Calderón Ormeño, Paola Güímac Tapia, Christine Fiorello and Mery Enciso.

The Gordon and Betty Moore Foundation is thanked for funding this research and my Ph.D. studies through a generous grant to the Botanical Research Institute of Texas (BRIT).

Thanks to all the BRIT staff and especially the AABP team, Keri McNew, Amanda Neill, Fernando Cornejo, Tiana Franklin, Jason Best and Asha McElfish for all the help they provided to make this project work out. I am also grateful to the whole WWF Areas team and especially George Powell for all the logistical support that was crucial for my work.

All camera trap work was carried out in collaboration with the WWF Areas project. The following people are thanked for helping with the camera trapping: Renate Leite Pitman, Rafael Mares, Angel Balarezo, Darío Cruz, Dario Cruz Junior, Alberto Escudero, Rene Escudero, Ernesto Gamarra, Lucas Huaymana, Javier Huinga, Armando Mendoza, Emeterio Nunoca, Juan Racua, Jhin Pierr Solis and Vicente Vilca.

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I am grateful to my committee at Texas A&M, Rodney Honeycutt, Raghavan Srinivasan, William Grant and Ben Wu, who understood the special circumstances of my work in Peru and gave me the freedom to pursue my research in a very independent way. Thanks to Jennifer Baker from Wildlife and Fisheries who helped me tackle all the administrative requirements while I was in the field. Without her help I probably would have missed several deadlines.

I would like to thank Peter Brown from NAVSYS for his great support with the TrackTags and his interest in finding new methods of adapting the TrackTags for tracking large mammals. Grant MacLean invested a lot of time into improving the signal processing algorithm for our difficult conditions under dense canopy. Julie Rosenberg and Chris Kochanny from Advanced Telemetry Systems led the development of the first TrackTag collars.

The Instituto Nacional de Recursos Naturales (INRENA) is thanked for granting permission for my research. This research was carried out under the following permits: 032-2005-INRENA-IFFS-DCB, OO63-2006-INRENA-IFFS-DCB, 029C/C-2007-INRENA-IANP and 014-2006-INRENA-IFFS-DCB.

I would also like to thank the long list of researchers who worked at Los Amigos during the last couple of years and who, with interesting discussions and wild parties, made life in the field a lot of fun. Thanks to everybody who helped us out with the tapir captures and other activities.

Thanks to all the members of the Tapir Specialist Group for many interesting discussions and the inspiration and motivation they gave me for my work.

The following persons are thanked for providing valuable input to various chapters of this dissertation: John Janovec, Louise Emmon, Kery McNew, Tiana Franklin, Amanda Neill, George Powell, Andrew Noss and Christine Fiorello.

I would like to thank my parents Verena and Werner Tobler for giving me the opportunity to pursue an academic career and for always encouraging my work in many parts of the world. Thanks to my mom for providing me with the perfect environment for writing this dissertation at her house in Switzerland.

Last but not least I would like to thank Samia Carrillo-Percastegui for her love, her patience, and for all her help in the field and during the time of analyzing the data and writing this dissertation.

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CHAPTER I
INTRODUCTION

Dissertation Outline and Objectives

In this first section I would like to give an overview of the topics addressed in my dissertation. The reader will notice that this dissertation has a somewhat broader scope than most dissertations, due to how this project evolved. In 2004 the Botanical Research Institute of Texas (BRIT) received a three-year grant from the Gordon and Betty Moore Foundation to start a project entitled "*Applying and Testing Innovative Technology to Strengthen Biodiversity Science and Conservation in the Andes to Amazon Region of Southeastern Peru*". As the title suggests, the project aimed at testing and applying new technologies to biodiversity research and conservation in the Peruvian Amazon. The project included various principal components in the fields of botany, wildlife ecology, entomology, GIS and biodiversity informatics. The main component of my involvement in the project was to evaluate new technologies for the research on large rainforest mammals, with a focus on the lowland tapir (*Tapirus terrestris*). The technologies used and discussed here are camera traps - cameras equipped with a motion sensor that automatically take photos when animals pass by - and a new type of GPS collar that is the first to work under the dense canopy of tropical forests.

This dissertation is divided into five main chapters, in two chapters I evaluate and discuss the technologies and in two chapters I show their application for studies of ungulates and tapirs in particular. There is one chapter on the diet of lowland tapirs that is not directly related to the development and testing of new technologies, but to the combination of botanical and mammal data collected through the different parts of the full, integrated BRIT.

Chapter II of this dissertation evaluates the usefulness of camera traps for inventories of terrestrial mammals in tropical forest. Mammal inventories are an important first step

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This dissertation follows the style of the *Journal of Applied Ecology*.

when evaluating the potential of an area for conservation or the current state of a protected area. Many gaps still exist in our knowledge of the distribution of many neotropical mammal species, and camera traps are an important tool that could help fill these gaps. Chapter III applies data from camera traps to investigate the ecology of five species of ungulates that are common throughout the Amazon. It shows how camera traps can be used to collect detailed information on occupancy rates, habitat use, activity patterns and the use of key resources such as mineral licks. Chapter IV looks at the diet of lowland tapirs and relates the diet to plant phenology. The potential of tapirs as seed dispersers is evaluated and discussed. Chapter V tests the performance of a new type of GPS collar in dense tropical forests by looking at the error distributions, success rates, possible data screening methods and the impact of biased data loss on home range estimators. Chapter VI uses data collected by GPS collars to investigate movement patterns, home range size, habitat use and the use of mineral licks by lowland tapirs. In the remainder of this introduction I will give a brief overview of the history and use of camera traps and GPS collars as well as the natural history of tapirs and the importance of mineral licks for large herbivores.

New Technologies for Research on Neotropical Mammals

Camera Traps

The use of animal-activated cameras goes back to the beginning of the 20th century when photographers used trip wires to take photographs of elusive animals (Cutler and Swann 1999). Researchers started using camera traps in the 1950s, but it was not until commercial models contained in waterproof housings and equipped with infrared or heat-motion sensors became available in the 1990s that researchers really started applying this new tool (Cutler and Swann 1999). The use of these modern camera traps by sport hunters in the United States to photograph game species, created a large market, drastically increasing the number of available models, and reducing prices. Nowadays, it is possible to purchase a 35 mm camera trap for under $100 and a digital model for $200, although features and quality as well as prices vary widely.

Seydack (1984) was probably the first to use automatic cameras to study rainforest mammals. He used six cameras with pressure plates set throughout a 6 km^2 study area in blocks of 1 km^2. He collected the data for a species inventory as well as to estimate bushbuck abundance and to identify individual leopards in Africa. Ten years later, Griffiths and van Schalk (1993) used camera taps to study rainforest mammals in Indonesia. They recognized that camera traps had a lot of potential to detect species presence and study behavior, activity patterns and abundance of elusive mammals (Griffiths and van Schalk 1993; van Schaik and Griffiths 1996). Shortly after, Ullas Karanth used camera traps set out over a large area combined with capture-recapture models to estimate tiger densities in several protected areas in India (Karanth 1995; Karanth and Nichols 1998). The methodology proposed by Karanth and Nichols (1998) was adopted widely for surveying a variety of different animal species and is currently probably the most common use of camera traps for wildlife research (Trolle and Kery 2003; Wallace *et al.* 2003; Maffei *et al.* 2004; Silver 2004; Di Bitetti *et al.* 2006; Jackson *et al.* 2006; Karanth *et al.* 2006; Soisalo and Cavalcanti 2006; Rios-Uzeda *et al.* 2007; Trolle *et al.* 2007). Other applications include mammal inventories (Gómez *et al.* 2001; Silveira *et al.* 2003; Trolle 2003b; Rovero *et al.* 2005; Srbek-Araujo and Garcia 2005; Azlan 2006; Giman *et al.* 2007; Kauffman *et al.* 2007), the study of activity patterns (Carthew and Slater 1991; van Schaik and Griffiths 1996; Bridges *et al.* 2004; Gómez *et al.* 2005; Azlan and Sharma 2006), and site occupancy studies (MacKenzie *et al.* 2005; Linkie *et al.* 2007).

A growing number of publications show the increased use of camera traps by researchers from all continents, studying a wide range of animal species in different ecosystems. Camera traps are ideal for studying elusive species or species that occur at low densities such as carnivores or forest ungulates. They can collect data on a large number of species simultaneously, operate 24 hours a day and often they require less work than other methods such as transects or track counts. They are easy to use and have less impact on the animal population studied than methods based on captures and radio telemetry.

GPS Collars

Radio telemetry was first used for wildlife studies in the 1960s and since then has become a popular method for studying habitat use, movement patterns and survival of a wide range of animal species (Kenward 2001). Today radio transmitters small enough to track beetles (Rink and Sinsch 2007) and large enough to put on elephants (Thouless 1995) are available. While transmitter and battery technology have greatly improved over the years (Rodgers 2001), the basic principle of radio telemetry has not changed. Collared animals are located by using directional antennas for obtaining bearings to the animal from at least two different known locations, thus allowing one to calculate the animal's location by triangulation (White and Garrott 1990). Tracking can be done from an airplane, a car, a fixed tower system or on foot, and often requires a significant amount of time and work. One of the main problems with radio telemetry in tropical forests is that the signal range is usually less than 2 km, making it very difficult to locate the study animals (pers. obs.). For most wide-ranging species, researchers therefore had to depend on aerial tracking, which is both expensive and dangerous (Rabinowitz and Nottingham 1986; Crawshaw 1995; Fragoso 1998).

In 1994 the Global Positioning System (GPS), consisting of 24 satellites and a network of ground control centers operated by the United States Department of Defense, became fully operational and available for public use (Rodgers 2001). Shortly after that the first GPS-based animal tracking devices became available (Rodgers *et al.* 1996; Moen *et al.* 1997; Rempel and Rodgers 1997). During the first years of operation, the U.S. military artificially degraded the signal quality (a process known as selective availability), making the system only accurate to about 100 m under good conditions (Moen *et al.* 1997). In May 2000 selective availability was removed, thus allowing civilian users to use the undegraded signal, with errors <10 m in open conditions (Hulbert and French 2001; Oderwald and Boucher 2003).

The first GPS collars were relatively heavy and only suitable for large animals. As with radio transmitters, the development of new microcontrollers and power supplies allowed for a decrease in weight for GPS collars and an increase in the number of locations that

can be recorded. Today GPS units are available in many different sizes, and are small enough for birds (Rose *et al.* 2005). GPS collars can be divided into two general classes, the ones that store positions in an internal memory and have to be retrieved to access the data, and the others that have a build in communication link (UHF radio, GSM cell phone network, ARGOS satellite) that allows researchers to download data on a regular time interval (Rodgers 2001). Store-on-board collars are usually cheaper but bear the risk that all data will be lost should the collar not be retrieved. GPS collars for large mammals are usually equipped with a radio transmitter that allows for locating the animal using regular radio tracking and most units have a timed or remote-controlled drop-off mechanism that automatically releases the collar, thus eliminating the need to recapture the animal to retrieve the data.

While GPS collars have been widely used in temperate regions and more recently also in the savannas of South America (Soisalo and Cavalcanti 2006; de Melo *et al.* 2007), they perform very poorly in tropical lowland forest with dense canopies. Rumiz and Venegas (2006) showed that while GPS collars worked in the dry forest of the Bolivian Chaco, they had a success rate of only 1-3% in the lowland forest of the Madidi National Park, Bolivia. Collars tested for a forest elephant study in central Africa had a success rate of 9.8% in hand-held trials in dense forest (Blake *et al.* 2001). The lack of any other studies using GPS collars in tropical lowland forests reflects the fact that few researchers have had success using them in such habitats. New technologies such as the one presented in this dissertation are needed to make GPS collars work in tropical forests.

The Lowland Tapir

Distribution and Status

Tapirs are ungulates of the order Perissodactyla. The family Tapiridae first appeared in North America during Eocene nearly 50 Million years ago with the genus *Tapirus* appearing in the Miocene 25 to 5 Million years ago (Eisenberg 1997). The four living species of tapirs occur in the tropics of Central America (Baird's tapir *T. bairdii*), South America (lowland tapir *T. terrestris* and mountain tapir *T. pinchauqe*) and Southeast

Asia (Malayan tapir *T. indicus*). The lowland tapir occurs from north-central Colombia and east of the Andes throughout most of tropical South America. It occurs mostly in tropical lowland rainforest but can also be found in seasonally dry habitats such as the Chaco of Bolivia and Paraguay. Lowland tapirs have been classified as vulnerable in the IUCN Red List of Threatened Species (IUCN 2008) and are listed in CITES Appendix II (CITES 2005). The major threats to the species are hunting and habitat destruction.

Tapirs are among the preferred game species for subsistence and commercial hunters throughout the Amazon (Redford and Robinson 1991; Vickers 1991; Bodmer 1995; Bodmer and Lozano 2001). They have a very low reproduction rate, and even a low hunting pressure quickly leads to a population decline (Peres 1996; Bodmer *et al.* 1997; Carrillo *et al.* 2000; Novaro *et al.* 2000; Peres 2001). They usually produce a single young born after a gestation period of 13 months. Under the best circumstances, a young can be born every 14 months but reproduction rates in the wild might be lower. Females become reproductive at the age of two and remain reproductive into their twenties (Padilla and Dowler 1994). This places the maximum productivity of a healthy female tapir at approximately 15 young in her lifetime, but very little data exist on the life expectancy and reproduction of tapirs in the wild.

Home Ranges, Movement Patterns, and Habitat Use

Very few studies have been conducted on movement patterns, home range size, and habitat use of lowland tapirs. Habitat use by lowland tapirs in tropical rainforests was studied by Bodmer (1990a) using harvest data, by Salas (1996) using track data, and by Herrera *et al.*(1999) using both track counts and radio telemetry. Ayala (2003) used radio telemetry to study lowland tapirs in the Chaco of Bolivia, and a large study is currently underway in the Atlantic rainforest of Brazil (Patrícia Medici, pers. comm.). Baird's tapirs were studied for over 10 years in the lowland rainforest of Costa Rica, first by Naranjo (1994) using tracks and then by Foerster and Vaughan (2002) using telemetry.

Home range size for lowland tapirs was reported to be between 190 and 300 hectares in the Chaco (Ayala 2003) and between 60 and 230 hectares for Baird's tapir in a lowland rainforest in Costa Rica (Foerster and Vaughan 2002). While Foerster and Vaughan (2002) found no seasonal changes in size or location of home ranges, they reported a change in relative habitat use within the range and correlated this with fruit availability. Salas (1996) also found seasonal differences in habitat use for lowland tapirs in Venezuela.

Key Food Species

Tapirs have a broad diet, feeding on a wide variety of plants and fruits (Terwilliger 1978; Janzen 1982a; Williams 1984; Bodmer 1991a; Naranjo 1995b; Salas and Fuller 1996; Tobler 2002) but use locally abundant fruit extensively when available (Bodmer 1990a; Fragoso 1997; Foerster and Vaughan 2002). Lowland tapirs were observed to eat fruit from over 150 species of plants (Bodmer 1991a; Rodrigues *et al.* 1993; Salas and Fuller 1996; Olmos 1997; Fragoso and Huffman 2000; Galetti *et al.* 2001). A study in a lowland rainforest in Venezuela showed that tapirs browsed on 88 plant species and consumed fruits of 33 species (Salas and Fuller 1996), and they appear to be selective in terms of browsing.

The importance of fruit in tapir diet seems to vary between study sites. Bodmer (1990a) showed that the diet of lowland tapirs in a tropical rainforest in Peru can consist of up to 33% fruit. In the lowland moist forest of Corcovado, Costa Rica, the percentage of fruits eaten by Baird's tapir varied between 3.2-12% from fecal analysis (Naranjo 1995b) and 12.4-22.3% from direct observations (Foerster 1998). Naranjo and Cruz (1998) found fruits to make up 6.2-8.1 % of the diet in several forest types from lowland moist forest to montane forests in Chiapas, Mexico, for the same species. Tobler (2002) The proportion of fruit in the diet of tapirs varied strongly between dry and wet seasons (Naranjo 1995b; Foerster 1998; Naranjo and Cruz 1998). This is most likely related to the strong difference of fruit availability between seasons in lowland rainforests (Altrichter *et al.* 2001).

Several studies showed that palm fruits are one of the most important resources for tapirs (Bodmer 1991a; Fragoso and Huffman 2000; Foerster and Vaughan 2002). Bodmer (1990a) found *Mauritia flexuosa* to be the single most important food item in the diet of tapirs in northern Peru. The distribution of these palm patches appear to strongly influence the movement patterns of tapirs.

Lowland tapirs seem to play an important role as long-distance seed dispersers, ingesting whole seeds and dropping them intact with their feces (Bodmer 1991a; Rodrigues *et al.* 1993; Fragoso 1997; Henry *et al.* 2000; Galetti *et al.* 2001; Fragoso *et al.* 2003). Bodmer (1991a) found that tapirs are the only Amazonian ungulate that regularly disperses seeds. But Janzen (1981) also found that Barid's tapir was an effective seed predator for two tree species in Guanacaste, Costa Rica.

Mineral Licks and Geophagy in Large Herbivores

Geophagy, the ingestion of soil, is a common behavior among herbivores and omnivores in all parts of the world (Emmons and Stark 1979; Jones and Hanson 1985; Moe 1993; Tracy and Mcnaughton 1995; Klaus *et al.* 1998).

Mineral licks, also called salt licks, natural licks, clay licks or, in Peru, *collpas*, are sites where animals come to eat soil material. These sites range in size from a few meters to several hundred meters in diameter (Klaus 1998; Klaus and Schmid 1998). During a study of two licks along the Los Amigos River, Dyana La Rosa (pers. comm.) found that they were visited by 12 species of mammals. Some of the most regular visitors were tapirs, white-lipped peccaries (*Tayassu pecari*), and red brocket deer (*Mazama americana*).

The most common explanations for geophagy are mineral supplementation (Jones and Hanson 1985; Kreulen 1985; Tracy and Mcnaughton 1995; Holdo *et al.* 2002), detoxification of secondary plant compounds (Oates 1978; Gilardi *et al.* 1999; Houston *et al.* 2001), and the treatment of acidosis (Kreulen 1985) and diarrhea (Mahaney *et al.* 1996; Krishnamani and Mahaney 2000). Several studies from different sites around the world suggest that sodium is the main element sought by animals visiting licks

(Tankersley and Gasaway 1983; Stark 1986; Moe 1993; Tracy and Mcnaughton 1995; Brightsmith and Munoz-Najar 2004). Other elements found in elevated concentration in lick soils are calcium, magnesium and potassium (Emmons and Stark 1979; Jones and Hanson 1985; Klaus *et al.* 1998). None of these explanations so far has been singled out as the main reason for lick use and it seems likely that geophagy has multiple benefits for the animal. One must remember, however, visiting licks is also associated with costs for the animal such as energy needed to get to the lick (Wiles and Weeks 1986), increased exposure to diseases due to increased contact between animals, as well as increased risk of predation and poaching (Hebert and Cowan 1971; Klaus *et al.* 1998). The benefits from visiting licks must outweigh these costs.

While many studies have analyzed chemical composition of lick soils, relatively few studies examined the impact of lick distribution on home range size and movement patterns of mammals. Moose in Alaska visit licks on their yearly migration routes and visit licks outside their home range (Tankersley and Gasaway 1983). Mountain goats in the Rocky Mountains used licks only once a year on their migration from their winter to their summer range (Hebert and Cowan 1971). On a study of white-tailed deer, Wiles and Weeks (1986) found no increase in density around licks which means that deer choose home ranges independent from lick locations and animals traveled several kilometers outside their home range to get to a lick. A tapir in the rainforest of Bolivia traveled up to 6 km outside of its home range to visit a mineral lick (Herrera *et al.* 1999). Tapirs in the same area visited licks most often between 18:00 h and 22:00 h and stayed less than 10 minutes per visit. Individual tapirs visiting a lick in Madre de Dios, Peru showed different patterns in their visits. Of the 12 individuals using the lick, some animals visited daily, while others were infrequent visitors (Montenegro 1998). Tapirs stayed at the lick for a few minutes or up to one hour, with an average duration of 23 minutes, and most visits occurred between 21:00 h and 3:00 h. Elevated levels of Na, Mg, Ca, and K were found in soil samples from this lick.

Study Area

Most of the research was carried out within the Los Amigos Conservation Concession (12°30' to 12°36' S and 70°02' to 70°09' W, elevation 250 to 320 m), a 1400 km^2 privately managed protected area in Madre de Dios, Peru (Figure 1). The concession was granted to the Associación para la Conservación de la Cuenca Amazonica (ACCA), a Peruvian NGO, in 2001 by the Peruvian Government. Until 2003 illegal loggers were cutting hardwoods, such as mahogany and Spanish cedar, inside the concession, and there was some hunting associated with that. However, since the logging was very selective, the forest is still in a fairly pristine state. This is evidenced by the presence of healthy populations of 11 different primate species and 31 species of large and medium-sized terrestrial mammals. The conservation concession is surrounded by several logging concessions that by law have to manage the forest in a sustainable way. Along the Madre de Dios River there are also mining concessions for small scale gold mining. Part of the more than 100 km trail system available for researchers is within active logging concessions. Some hunting is still taking place outside the concession by miners and loggers, but logging and hunting inside the concession have been stopped. The concession protects the watershed of the Los Amigos River, which is a tributary to the Madre de Dios River. The area belongs to the Southwest Amazon moist forests ecoregion (Olson *et al.* 2001), and the main vegetation types are *terra firme* and floodplain forests, palms swamps and patches dominated by bamboo. Successional forests occur along the meandering rivers. Over 2500 plant species have been documented in the area (J. Janovec pers. com., and http://atrium.andesamazon.org).

The climate is tropical with mean annual rainfall between 2500 and 3500 mm and a dry season from May to September and a rainy season during the months of November through February. Mean annual temperature is 24°C with a range from 10 to 38°C (Figure 2).

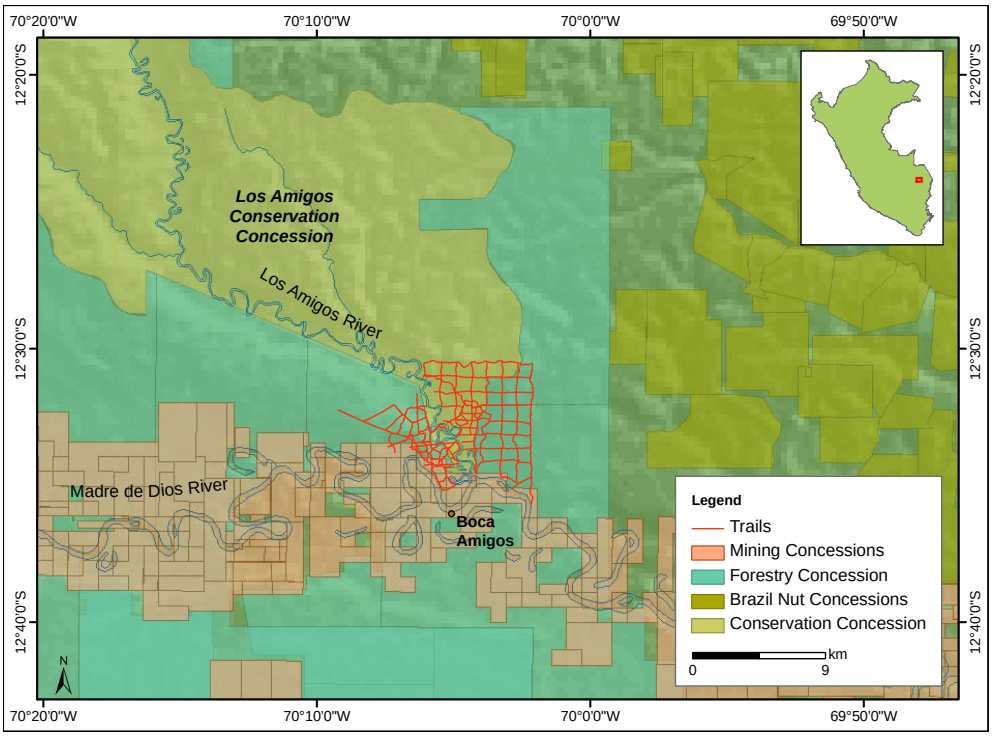

Figure 1: Map of the Los Amigos Conservation Concession and surrounding forestry and mining concessions. The main study area was in the southeastern part of the concession where the trail network is located.

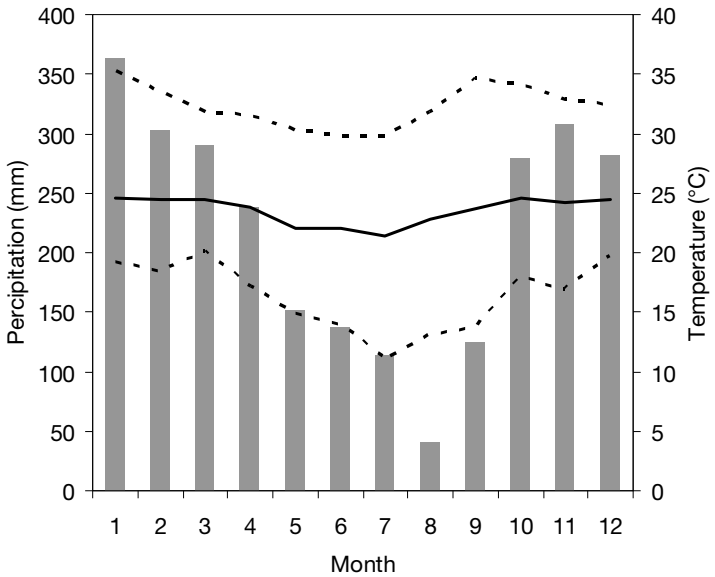

Figure 2: Precipitation and temperature patterns recorded at the Los Amigos Biological Station between November 2000 and January 2008. Bars show mean precipitation values andlines show minimum, average and maximum temperature values. Source http://atrium.andesamazon.org

CHAPTER II
AN EVALUATION OF CAMERA TRAPS FOR INVENTORYING LARGE AND MEDIUM-SIZED TERRESTRIAL RAINFOREST MAMMALS *

Synopsis

Mammal inventories in tropical forests are often difficult to carry out and many elusive species are missed or only reported from interviews with local people. Camera traps offer a new tool for conducting inventories of large and medium-sized terrestrial mammals. We evaluated the efficiency of camera traps based on data from two surveys carried out at a single site during two consecutive years. The survey efforts were 1440 and 2340 camera days, and 75% and 86% of the 28 large and medium-sized terrestrial mammal species known to occur at the site were recorded. Capture frequencies for different species were highly correlated between the surveys and the capture probability for animals that passed in front of the cameras decreased with decreasing size of the species. Camera spacing and total survey area had little influence on the number of species recorded, with survey effort being the main factor determining the number of recorded species. Using a model, we demonstrated the exponential increase in survey effort required to record the most elusive species. We evaluated the performance of different species richness estimators on this dataset and found the Jackknife estimators generally to perform best. We give recommendations on how to increase efficiency of camera trap surveys exclusively targeted at species inventories.

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Introduction

Mammal inventories serve a multitude of purposes: they show the diversity at a specific site, allow for comparison among sites, help refine distribution maps for individual species and can be used to evaluate the impact of human activities on mammal communities. A good knowledge of the presence and distribution of species is crucial for planning and evaluating conservation strategies for a region. However, despite years of research throughout the Amazon, there are few complete mammal inventories and our knowledge on the distributions of rare and elusive species is still poor (Voss and Emmons 1996). Methods commonly used for mammal inventories are line transects, direct observations, identification of tracks and feces, trapping and interviews with local people (Voss and Emmons 1996; Voss *et al.* 2001; Trolle 2003a; Mendes Pontes 2004; Haugaasen and Peres 2005). While line transects can be used to survey the density of relatively abundant mammal species, they often fail to record rare and elusive species such as small carnivores, anteaters and armadillos (Voss and Emmons 1996) .

The use of camera traps for studying terrestrial mammals has become increasingly popular in recent years as camera technology has improved and equipment costs have decreased. Applications range from collecting species inventories (Maffei *et al.* 2002; Silveira *et al.* 2003; Trolle 2003b; Srbek-Araujo and Garcia 2005; Azlan and Lading 2006), to studying activity patterns (van Schaik and Griffiths 1996; Gómez *et al.* 2005; Azlan and Sharma 2006), and estimating animal density (Mace *et al.* 1994; Karanth and Nichols 1998; Sweitzer *et al.* 2000; Trolle and Kery 2003; Silver *et al.* 2004). Silveira et al. (2003) concluded that camera trap surveys were the most appropriate and accurate method for mammal inventories in the open savannas of Emas National Park in Brazil when compared with line transects and track counts. In a study on forest antelopes in the Udzungwa Mountains of Tanzania, camera traps recorded species rarely encountered in census walks (Rovero *et al.* 2005). Records from camera traps in Tanzania significantly extended the known range for the endangered Jackson's mongoose (*Bdeogale jacksoni*) (De Luca and Rovero 2006). Photographs from camera traps provide reliable records of

a species presence, and they can be sent out for verification by experts (see Meijaard *et al.* 2006).

When conducting any inventory, it is important to evaluate its completeness to estimate how many more species might be detected by further sampling effort (Magurran 1988). An estimate of the completeness of an inventory is especially important when comparing species diversity among sites or when looking at changes in species composition over time. Species accumulation curves and diversity estimators are commonly used to address this issue (Soberon and Llorente 1993; Colwell and Coddington 1994). Species accumulation curves plot the cumulative number of species detected against the sampling effort per unit time, which in the case of camera traps can be survey days or camera days (the number of survey days multiplied by the number of cameras used). The curve reaches an asymptote when all species from the focal taxa have been recorded. Various methods have been developed to estimate the true number of species in an incomplete survey and to assess the completeness of the inventory (Soberon and Llorente 1993; Colwell and Coddington 1994; Colwell *et al.* 2004). These methods can be divided in to two broad classes: species richness estimators based on extrapolation of species accumulation curves and non-parametric estimators related to capture-recapture models (Colwell and Coddington 1994). The latter usually perform better in comparative studies (Walther and Moore 2005). In this study we report the results of two camera trap based inventories, evaluate the survey effort needed to record a certain percentage of the total species assemblage and test the performance of different non-parametric estimators to evaluate completeness of camera trap surveys.

Study Area

This study was carried out in mostly primary lowland Amazonian moist forest in southeastern Peru. About two thirds the study site were within the Los Amigos Conservation Concession (12°30' to 12°36' S and 70°02' to 70°09' W, elevation 250 to 320 m), a 1400 km^2 privately managed protected area, with the remainder falling within two active logging concessions. Mean annual rainfall is between 2500 and 3500 mm

with a marked dry season from June to September and a rainy season during the months of November through February. Mean annual temperature is 24°C with a range from 10 to 38°C.

Three major vegetation types can be distinguished in the study area: *terra firme* forests, floodplain forest and palm swamps dominated by the palm *Mauritia flexuosa*. Cameras were placed in *terra firme* and floodplain forests only, because the extent of palm swamps is very limited within the study area. The floodplain forest is occasionally inundated during the rainy season from December to March but there was no inundation during the time of the surveys reported here.

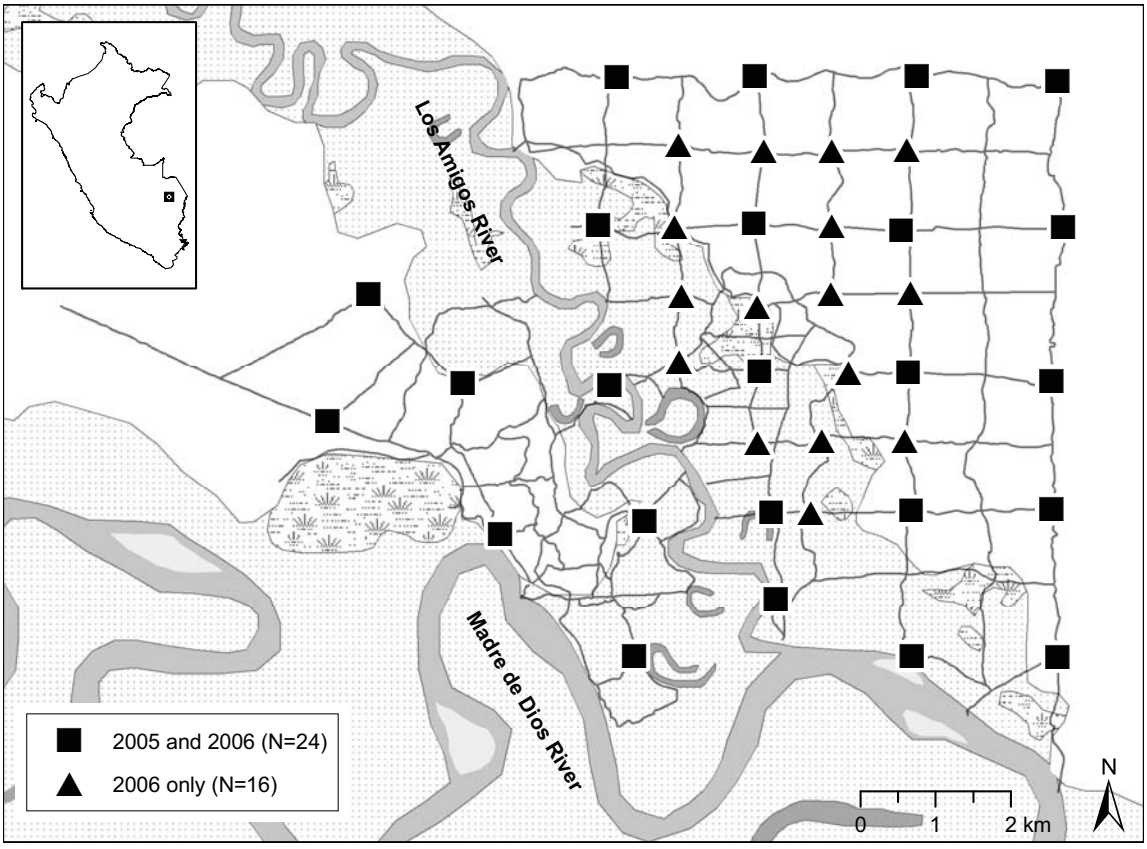

Figure 3: Study area and location of camera stations along the trail system. Dotted area indicates floodplain forest while the white area is *terra firme* forest.

Materials and Methods

Camera Trap Surveys

Two 60-day camera trap surveys were carried out from 14 September to 13 November 2005 and from 16 August to 15 October 2006, at the end of the dry season and the beginning of the rainy season. The surveys were designed to meet the requirements for estimating jaguar (*Panthera onca*) density (Silver 2004). In the 2005 survey, 24 camera stations were set out in a 2 km grid along the study site's trail system (Figure 3) covering an area of approximately 50 km^2. For the 2006 survey, we used the same camera locations as in 2005, but added 16 more camera stations at a 1 km interval in a central sub-area. In 2006 we excluded one camera station from the analysis because the cameras were malfunctioning, leaving a total of 39 stations.

Each camera station included paired cameras, facing one another on respective sides of a trail, allowing the cameras to photograph both sides of an animal. Cameras were set at an average height of 50 cm above ground. We used Deercam (NonTypical Inc.) passive infrared cameras, which were sealed with extra silicon and equipped with an aluminum roof for better protection from rain. Small silica bags were placed inside the camera housing to further reduce damage from moisture. The delay between pictures was set to five minutes and the sensitivity of the infrared sensor was set to high. Cameras were operating 24 hours a day and were checked every five days to replace film and batteries if necessary.

Data Analysis

All images were scanned and entered into Camera Base, an Access database designed for managing camera trap survey data (Tobler 2007). For every photograph the station, date, time and the species were recorded. To evaluate the effectiveness of our camera trap surveys for inventorying mammal species, a sub-set of all photographs including only large and medium-sized (weight >1 kg) terrestrial mammals were used, therefore excluding arboreal species, small rodent species, and mostly aquatic or riverine species (*Pteronura brasiliensis, Lontra longicaudis* and *Hydrochoerus hydrochaeris*).

We calculated the capture frequency of a given species as the number of photos / 1000 camera days, and used a Spearman rank correlation for comparisons between the two surveys. The data were filtered to exclude images of the same species at the same station within a period of one hour in order to make sure that events were independent, since some species (e.g. white-lipped peccaries *Tayassu pecari*) would spend a long period of time in front of a camera.

To evaluate the effect of species size on their capture probability, we calculated the percentage of times both cameras took a picture versus only one of the two cameras at a station and compared that to body weight based on data taken from Emmons & Feer (1997). Data from both surveys were pooled for the analysis and we only included the 14 species with samples of 15 photos or more, after excluding cases where an animal had walked behind one of the cameras at the station. We used a Spearman rank correlation to evaluate the relationship between body weight and percentage of events with pictures from both cameras.

To look at the effect of camera spacing and grid size on the inventory results, we sub-sampled the data from 2006 into two groups. The first group contained 22 stations spaced out in a regular grid at 1 km interval, covering an area of approximately 15 km^2. The second grid contained 23 stations spaced out at 2 km covering the full study area. Both grids had the same number of cameras in each habitat type.

We compared the performance of eight species diversity estimators: the non-parametric abundance based estimators ACE and Chao 1, and the non-parametric incidence based estimators ICE, Chao 2, Jackknife 1, Jackknife 2, Jackknife 3 and Jackknife 4 (Chao 2004). Since non-parametric species richness estimators are directly related to closed population capture-recapture models they underlie some of the same assumptions. They assume that the community composition does not change over the time of the study (closure) and the Jackknife estimators assume that there is no temporal variation in capture probability for all species (Burnham and Overton 1979; Chao 2004). With survey length of 60 days these assumptions should be met. We used EstimateS (Colwell 2006) to calculate rarefaction curves and most of the species estimators. The Jack 3 and

Jack 4 estimators were implemented with Visual Basic for Applications (VBA) in Excel. For all randomizations we used 1000 runs. To calculate different incidence-based species richness estimators, we treated each survey day as a sample, resulting in 60 samples for each survey. To compare the two surveys we plotted the results against the number of camera days. To evaluate the completeness of our surveys and the accuracy of the total number of species estimated by different estimators, we compared the number of species against a list of known species from the study area (Leite Pitman 2007).

To investigate the relationship between capture frequency and the number of camera days required to register a species, we used a simple binominal model:

$$P(X = k) = \frac{n!}{k!(n-k)!} p^k (1-p)^{n-k}$$

with *k*=number of successes, *n*= number of trials and *p*=probability of success.

In our case *p* is the average number of pictures per camera day for a given species, and *n* is the total number of camera days. By using a 5% probability of taking no photograph at all, we determined the number of camera days needed to collect at least one photograph for a species with a specific capture frequency, within a 95% confidence limit. For this case *k*=0 and P(X=0)=0.05 reducing the equation to:

$$0.05 = (1-p)^n$$

Solving the equation for n gives the following relationship:

$$n = \frac{\ln(0.05)}{\ln(1-p)}$$

Results

Capture Frequencies and Species List

During the 2005 survey we obtained 508 photographs of 21 species of mammals, during a total of 1440 camera days (Appendix A). In 2006 we obtained 814 photographs of 27 species of mammals, during a total of 2340 camera days. We excluded three species of

mammals from our analysis of the 2006 survey, because they were arboreal or small mammals; the common squirrel monkey (*Saimiri boliviensis*), the South-American red squirrel (*Sciurus spadiceus*) and the spiny rat (*Proechimys sp.*). A total of 28 species of large and medium-sized terrestrial mammals have been reported for the area (Leite Pitman 2007). The camera traps successfully registered all species of large mammals, with an overall completeness of the surveys of 75% (2005) and 86% (2006) for large and medium-sized mammals. The most commonly photographed species were white-lipped peccaries, lowland tapirs (*Tapirus terrestris*) and brown agoutis (*Dasyprocta punctata*). The most commonly photographed cat species were jaguars and ocelots (*Leopardus pardalis*). All species recorded exclusively in 2006 were represented by only 1-3 photographs, indicating their low capture probabilities. Capture frequencies for all species were highly correlated for the two surveys (Spearman's rho=0.883, $p<0.0001$, N=24), indicating that capture frequencies are species specific.

Table 1: The influence of camera trap spacing on the number of medium and large terrestrial mammal species registered during a 60-day survey in the Peruvian Amazon. .

	Stations	Camera Days	Floodplain	*Terra Firme*	Species	terr. Mammals
2 km grid	23	1380	8	15	32	23
1 km grid	22	1320	8	14	30	22
Total	39	2340	14	25	33	24

The data comes from two nested camera grids run simultaneously in the same area, one with 2 km camera spacing and the other one with cameras set 1 km apart.

Our data show that body weight had a strong positive correlation with the number of times both cameras at a station took a picture (Figure 4). This indicates that small animals are more likely to pass in front of a camera without triggering a picture and will therefore have a lower capture probability.

Camera spacing and grid size did not influence the survey success (Table 1). With identical survey effort almost the same number of species was obtained with the two different designs. All species recorded by only one of the two grids (jaguarundi (*Puma*

yagouarundi), crab-eating raccoon (*Procyon cancrivorus*) and Brazilian rabbit (*Sylvilagus brasiliensis*)) had very low overall capture rates.

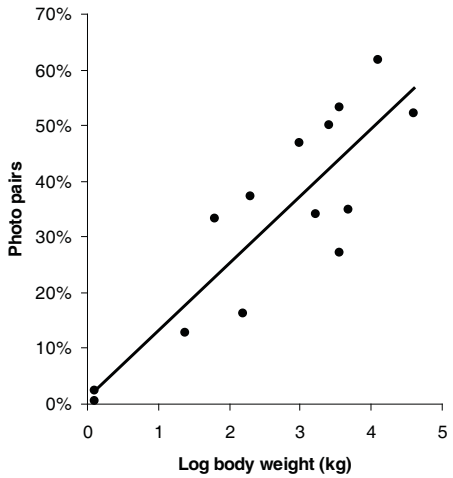

Figure 4: Relation between body weight and the percentage of times that both cameras at a station took a picture (Spearman's rho=0.811, $p<0.0001$, N=14).

Species Richness Estimators

The rarefied species accumulation curves for the 2005 and 2006 surveys have very similar shapes. Neither of the curves had leveled off, but the 2006 survey was clearly more complete than the 2005 survey. Figure 5 shows the behavior of the different species richness estimators with increasing survey effort. ACE and ICE are almost identical, probably because the number of individuals per sample most of the time is zero or one and hardly ever more than three or four, adding little extra information by using abundance instead of incidents. For the 2006 survey these estimators reach an asymptote at around 2000 camera days, but the estimated total number of species is too low. Chao 1 and Chao 2 are also almost identical. The estimated number of species reaches a maximum, slightly below the known number of species, at around 1600 camera days and then declines as the survey coverage increases. The Jackknife estimators show an interesting pattern. The higher order estimators (Jack 4 and Jack 3) give good results for the 2005 survey and up to about 1200 camera days in the 2006

survey but then become increasingly unreliable and actually show estimated values smaller than the number of observed species (S_{obs}). Jack1 gives the most reliable estimates for large numbers of camera days. Table 2 gives an overview of the performance of different estimators under different sample coverage (percentage of species detected in a survey). We can see that most estimators are lower than the true number of 28 species. However all estimators perform better than S_{obs} except for the two estimators Jack 3 and Jack 4 at a sample coverage of 80% and higher. In general the Jackknife estimators seem to give the best results followed by the ICE and ACE estimators. The two Chao estimators performed poorly.

Table 2: Observed and estimated species richness under different sampling intensity for two camera trap surveys in the Peruvian Amazon.

	2005				2006						
Days	8	17	33	60	5	7	13	26	36	51	60
Camera Days	192	408	792	1440	195	273	507	1014	1404	1989	2340
S_{obs}	12.2	15.4	18.2	21.0	13.4	15.3	18.5	21.1	22.3	23.5	24.0
Individuals	33	70	135	246	30	42	77	155	124	304	357
Chao 1	16.7	18.6	22.0	26.9	18.5	19.8	21.4	23.9	25.2	25.1	24.8
Chao 2	17.5	18.9	26.2	26.8	18.6	19.8	21.4	23.8	25.2	25.1	24.7
ACE	18.9	21.4	26.2	**27.3**	19.2	19.9	21.4	23.4	24.4	25.6	26.1
ICE	19.0	21.4	22.7	**27.3**	21.0	21.0	21.8	23.5	24.5	25.6	25.9
Jack 1	16.5	19.4	22.5	25.9	18.7	20.4	22.6	24.6	25.8	26.8	**27.0**
Jack 2	18.1	21.2	25.0	28.8	20.7	22.2	23.8	26.2	**27.6**	**27.7**	**27.0**
Jack 3	18.9	22.7	26.8	30.8	21.5	23.1	24.2	**27.6**	28.7	26.9	25.2
Jack 4	**19.4**	**24.0**	**28.1**	31.8	**21.9**	**23.6**	**24.5**	28.9	28.7	24.8	22.5
Coverage	44%	55%	65%	75%	48%	55%	66%	75%	80%	84%	86%

The number of species believed to be present in the study area is 28. Bold numbers indicate the best species richness estimation.

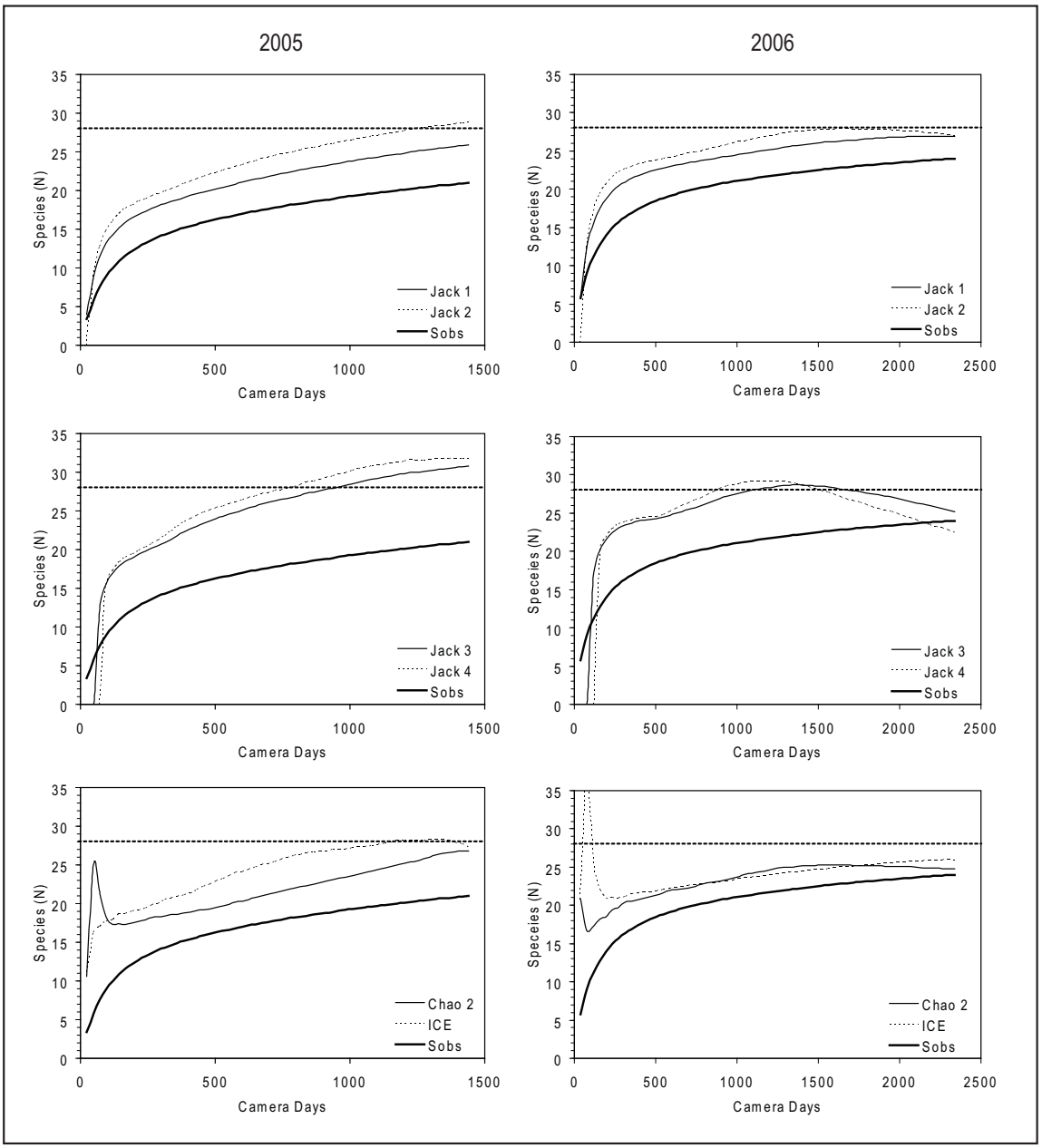

Figure 5: Comparison of different species estimators for two camera trap surveys carried out at the same site in two different years. The known number of species for the site is 28.

Model for Capture Probability

The species accumulation curves show that it takes only 400 to 500 hundred camera days to obtain a record of the most common species. It is the more elusive species that determine how much time is needed to complete a survey, and often those are the species of most interest. Figure 6 graphically shows the relationship between capture frequency and the time needed to obtain at least one photograph. We can see that the required sampling effort drastically increases once the frequency drops below 3/1000 camera nights. For a frequency of 2/1000 camera nights 1500 camera nights are required and for a frequency of 1/1000 camera nights 3000 camera nights are needed to register the species with a 95% probability.

Looking at the capture frequencies (Appendix A) we see that in our case about half of the species are fairly common with a capture frequency of four and above; while the other half of the species can be considered elusive and will require a large sampling effort. We calculated the probability to obtain at least one photograph based on the sampling effort for the 2005 and 2006 survey for the six rarest species and found that all the species missed in 2005 had a very low capture probability (Table 3).

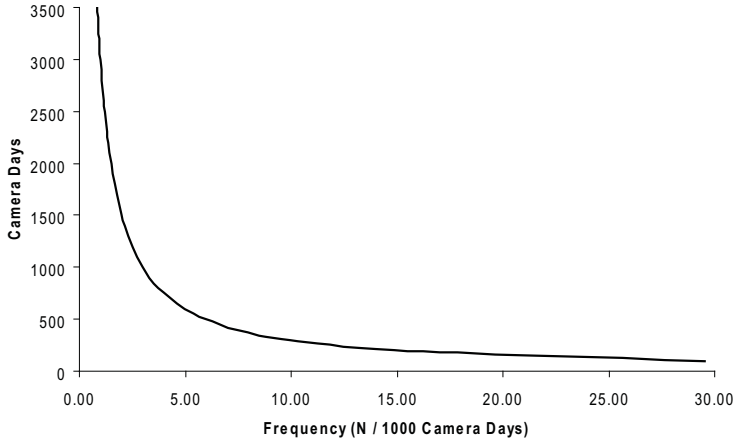

Figure 6: Number of camera days required to register a species with a 95% probability given a certain capture frequency.

Table 3: The probability of obtaining at least one photograph for the most elusive species in our study site for 1440 and 2340 camera days based on a binomial model.

Species	2005	2006	Freq. Total	Prob. 2005	Prob. 2006
Procyon cancrivorus		1 (0.43)	0.26	0.32	0.46
Myrmecophaga tridactyla		2 (0.85)	0.53	0.53	0.71
Puma yagouarundi	1 (0.69)	1 (0.43)	0.53	0.53	0.71
Dasypus novemcinctus	1 (0.69)	2 (0.85)	0.79	0.68	0.84
Sylvilagus brasiliensis		3 (1.28)	0.79	0.68	0.84
Tamandua tetradactyla	1 (0.69)	2 (0.85)	0.79	0.68	0.84
Nasua nasua	2 (1.39)	2 (0.85)	1.06	0.78	0.92

The first two columns show the number of events and capture frequencies (captures / 1000 camera days) registered for the two surveys (2005 and 2006). The third column shows the combined capture frequencies from the two surveys which were used to calculate the probabilities.

Discussion

Inventory Efficiency

Our results demonstrate the effectiveness of camera traps for inventorying large and medium-sized terrestrial mammals in tropical forests. Our cameras successfully registered 86% of the species known for the area during a period of only two months. Of the remaining species all are extremely rare and are only known from one or two records in the study area. The pacarana (*Dinomys branickii*) has been photographed in the study area before, but might occur at a low density. Grisons (*Galictis vittata*) and southern naked-tailed armadillos (*Cabassous unicinctus*) were recorded in camera trap studies at other sites (Leite Pitman 2007, G. Ayala and A. Paviolo pers. com.), but seem to be rare at our site with very few sightings over the last several years. Bush dogs (*Speothos venaticus*) have only been observed twice over the last three years. All of these species are poorly known by local people. Out of three published inventories from the same region, only one reported records of the bush dog and the southern naked-tailed armadillo, thus showing the difficulty of recording these species (Voss and Emmons 1996). The sampling period for those three inventories were two, three and 21 years and

the total number of large and medium-sized mammals reported were 19, 25 and 27 respectively. This shows the high efficiency of camera traps for rapid inventories.

Our results show that it takes a substantial survey effort to register some species. Several species had less than three photos taken during the 3840 camera days of both surveys combined. Other studies using camera traps for species inventories recorded 57% of the total number of species (16 of 28 species, 1035 camera days) in Emas National Park, Brazil (Silveira *et al.* 2003), and 80.9% (17 of 21 species, 1849 camera days) in the Atlantic forest of Brazil (Srbek-Araujo and Garcia 2005). Trolle & Kery (2005) recorded 23 species of large and medium-sized mammals in only 504 camera days in the Pantanal of Brazil. In a survey of a secondary forest in Malaysia, the species accumulation curve leveled off at 25 species after about 4600 camera days (Azlan 2006). Maffei *et al.* (2002) registered between 14 and 23 species at three sites in the Bolivian Chaco and the number of species was clearly related to the survey effort. However, even at a site with 4815 camera days and 23 species, there were several species that were only represented by one photograph, showing the difficulty of detecting rare species. For programs that aim to monitor the presence of a species or the community composition over time, or compare species diversity between different areas, it is important to keep in mind that a large survey effort is needed to register certain species and that the lack of photographs of a species does not automatically mean that the species is not present.

Capture frequencies for our two surveys are highly correlated indicating that these frequencies are species specific. While capture frequencies can give an idea of the relative abundance of different species, there is an ongoing discussion among scientists about the reliability of this index (Carbone *et al.* 2001; Carbone *et al.* 2002; Jennelle *et al.* 2002). We believe that capture frequencies are a relatively poor index for relative abundance among surveys or for comparing relative abundance of species within surveys due to a variety of factors such as species specific behavior (e.g. use or avoidance of trails (Trolle and Kery 2005), partly arboreal versus exclusively terrestrial, or habitat specialist versus generalist), species size (large animals are more likely to trigger the cameras), home range size (animals with larger home ranges move around more and

have more cameras within their home ranges), or simply stochastic variation as can be seen when looking at the large differences in capture frequencies for several species between the two surveys in this study.

Performance of Species Richness Estimators

All species richness estimators had a negative bias, but correctly indicated that some species were still missing in the samples. Our data show a very high heterogeneity in capture frequencies among species, with capture frequencies ranging from 0.4 to 66. The performance of the different estimators for this dataset supports results obtained from simulated data, where the Jackknife estimators performed best when heterogeneity in capture probability due to spatial distribution or movement of animals was introduced to the data (Brose *et al.* 2003; Brose and Martinez 2004). In such circumstances, Brose et al. (2003) recommend using Jack 4 for sample coverage of 26-35%, Jack 3 for coverage up to 50%, Jack 2 for coverage up to to 74% and Jack 1 for samples with a coverage of 75-96%. This sequence of using lower order Jackknife estimators with increasing sample coverage works well for our data and the point at which switching to a lower order Jackknife estimator is necessary can usually be determined by a decline in the estimated number of species. For our data Jack 4 performs well up to a sample coverage of approximately 65%.

Survey Design

Camera traps are still most frequently used in surveys to estimate the abundance of large cats (Wallace *et al.* 2003; Silver *et al.* 2004; Di Bitetti *et al.* 2006; Jackson *et al.* 2006; Karanth *et al.* 2006). However, these surveys often produce a reliable inventory of all large and medium-sized mammals as a useful by-product. Our survey was designed to meet the requirements needed for estimating jaguar density using capture-recapture models (Silver 2004; Silver *et al.* 2004) with camera stations set at regular intervals on trails, in pairs to photograph both sides of the animal and not being moved during the two month survey period. If the goal of a survey is exclusively to produce a species inventory, it is possible to use a more flexible design and reduce costs while increasing

efficiency. Each station could be equipped with a single camera instead of a pair of cameras, reducing the number of cameras needed by half. Based on our data this will reduce the capture probability especially for small species; however, for most species this reduction will be less than 50% and therefore will increase efficiency.

Our data indicate that camera spacing and the area covered have little impact on the survey results. Therefore surveys for inventory purposes can be conducted on a relatively small trail system with a high camera density to achieve the required camera days. It is important however, to make sure that all the major habitat types are covered since some species might be more abundant or even restricted to one habitat type.

To increase the probability of catching species that rarely use trails or are habitat specialists, cameras can be set at sites targeting specific species, such as animal trails, little streams, mineral licks, dens and fruiting trees. Other options are to bait camera stations to attract animals (Long *et al.* 2003; Trolle and Kery 2005) or to move cameras if the number of photos is very low or it seems that a large number of photographs result from a single species or individual passing by the camera repeatedly (Srbek-Araujo and Garcia 2005). Unfortunately some of these designs may violate assumptions for the species richness estimators, resulting in more biased estimates.

CHAPTER III
THE ECOLOGY OF AMAZONIAN UNGULATES REVEALED BY CAMERA TRAPS

Synopsis

We studied the habitat use, activity patterns and the use of mineral licks of five species of Amazonian ungulates. Data was collected with cameras traps set out in a regular grid at two different study sites, with repetitions at one of the sites, as well as at five mineral licks. White-lipped peccaries had the largest number of photos taken followed by lowland tapirs. Occupancy analysis showed that grey brocket deer almost exclusively occur in *terra firme* forests, and in some surveys, that white-lipped peccaries used floodplain forest more frequently. All other species showed no habitat preference. Occupancy rates were lowest for the grey brocket deer and the collared peccary and highest for the white-lipped peccary and the tapir. Both peccary species as well as the grey brocket deer were strictly diurnal while the tapir was nocturnal. The red brocket deer was active day and night with a period of low activity at mid day. Tapirs were the species with the highest number of visits to mineral licks followed by white-lipped peccaries and red brocket deer. Collared peccaries were only registered on three occasions and grey brocket deer were never seen at a lick. The number of visits differed between licks, with some licks being preferred by one species and others by another.

There was a high overlap in the distribution of species, indicating that resource partitioning does not take place on a spatial scale. The two brocket deer species differ greatly in their activity patterns, while diet and space use might be a more important factor for the other species. Our results show the great potential camera traps have for studying large mammals in tropical forests. A wide range of data could be collected on five species simultaneously, revealing important information on their ecology.

Introduction

Five species of ungulates commonly occur throughout the Amazon basin: the red brocket deer (*Mazama americana*), the grey brocket deer (*Mazama gouazubira*), the collared peccary (*Pecari tajacu*), the white-lipped peccary (*Tayassu pecari*) and the lowland tapir (*Tapirus terrestris*). These five species are sympatric in most parts (Emmons and Feer 1997), and make up roughly 50 percent of the average mammal biomass in the Amazon. All of them are preferred game species accounting for up to 60 percent of the game consumed in the region (Bodmer 1995; Alvard *et al.* 1997; Peres 2000). Ungulates, therefore, provide the most important source of protein for rural populations throughout the Amazon and provide a substantial amount of income to rural households (Bodmer and Lozano 2001). The five species respond differently to hunting pressure; while populations of white-lipped peccaries and tapirs drastically decline and often go extinct, collared peccaries and the two deer species can maintain viable populations and sustainable hunting is possible (Peres 1996; Alvard *et al.* 1997; Hurtado-Gonzales and Bodmer 2004; Peres and Palacios 2007). However, even for the latter group, density drastically declines with increased hunting pressure (Peres 1996; Peres 2000).

Ungulates are not only important game species, but they also shape the diversity and structure of tropical forests. Peccaries and brocket deer are seed predators, destroying large quantities of seeds through mastication or digestion (Bodmer 1991b). Tapirs, on the other hand, are able to disperse large numbers of viable seeds over long distances (Fragoso and Huffman 2000; Henry *et al.* 2000; Chapter IV). Tapirs can also change the sapling community by selective browsing (Foerster 1998), and peccaries can kill large numbers of saplings through rooting and digging for seeds and invertebrates (Kiltie and Terborgh 1983).

Despite their ecological and economic importance, few studies exist on the ecology of Amazonian ungulates. The two species of peccary differ greatly in their social behavior and use of space. White-lipped peccaries from large herds of 30 to 300 individuals,

while collared peccary herds usually contain less than 15 individuals (Kiltie and Terborgh 1983; Peres 1996; Fragoso 1999; Keuroghlian *et al.* 2004). White-lipped peccaries range over areas from 10 to 100 km^2 and have been reported to follow seasonally available resources (Fragoso 1998; Carrillo *et al.* 2002; Keuroghlian *et al.* 2004). Collared peccaries have much smaller home ranges (0.1 to10 km^2) and usually show little seasonal variation in home range size (Fragoso 1999; Keuroghlian *et al.* 2004). Both species are mostly frugivorous, but have a broad diet including plant material such as leaves, tubers and roots, as well as invertebrates and even some vertebrates (Beck 2005). The diets of both species largely overlap (Bodmer 1991a; Fragoso 1999; Beck 2005), but the lower bite force of collared peccaries makes some food items (mainly hard seeds) unavailable to them (Kiltie 1982). However, most authors suggest that niche differentiation for the two species occurs on a spatial level through habitat use and the spatial scale at which resources are used (Bodmer 1991a; Fragoso 1999; Keuroghlian *et al.* 2004). Brocket deer presumably have small home ranges of less than 1 km^2 (Maffei and Taber 2003), but no data are available from the Amazon. Both species are frugivores, but their diet can also include large quantities of leaves, flowers, and other plant material as well as fungi (Branan *et al.* 1985; Bodmer 1991a; Gayot *et al.* 2004). They are generalists, feeding on a large variety of plant species, with the grey brocket deer eating more fruit than the red brocket deer and being more selective (Gayot *et al.* 2004). Lowland tapirs have home ranges of 1.5 to 4 km^2 with little seasonal variation in size and some overlap between different individuals (Ayala 2003). Their diet contains larger quantities of browse than the diet of the other ungulate species, but they also feed extensively on fruit when available (Bodmer 1991a; Salas and Fuller 1996; Fragoso and Huffman 2000; Henry *et al.* 2000; Chapter IV).

The lack of available information is partly due to the difficulty of studying ungulates in tropical forests. Most studies so far have relied on direct observations (e.g. line transects) or signs (e.g. tracks, feces) to study habitat use by ungulates (Bodmer 1991a; Peres 1996; Salas 1996; Rivero *et al.* 2005). Few studies used radio telemetry to track animals (Fragoso 1999; Herrera *et al.* 1999; Carrillo *et al.* 2002; Foerster and Vaughan 2002;

Ayala 2003; Keuroghlian *et al.* 2004). Camera traps have gained increasing popularity among biologists in recent years as a new, non-invasive tool to collect data on elusive mammals. While their most popular use has been to estimate the density of large cats in conjunction with capture-recapture methods (e.g. Karanth 1995; Trolle and Kery 2003; Silver *et al.* 2004), they are also being used for mammal inventories (Maffei *et al.* 2002; Srbek-Araujo and Garcia 2005; Tobler *et al.* in press), to study activity patterns (Gómez *et al.* 2005; Azlan and Sharma 2006), and to evaluate the distribution and occupancy of rare species (MacKenzie *et al.* 2005; Linkie *et al.* 2007). However, they have only rarely been used to collect a range of data on the ecology of one or several species (Di Bitetti *et al.* 2006; Arispe *et al.* in press). In this study we used camera traps to study various aspects of the ecology of Amazonian ungulates including: 1) habitat use, 2) activity patterns, 3) use of mineral licks and 4) occupancy at two sites. This information allows one to evaluate the resource partitioning between the five species.

Study Area

This study was conducted at two different sites in the department of Madre de Dios in southeastern Peru. The first site was the Los Amigos Conservation Area, a 1400 km^2 private protected area along the Madre de Dios and the Los Amigos rivers. Our study area at this site included part of the concession and two adjacent active logging concessions (12°57' to 12°36' S and 70°02' to 70°09' W, elevation 250 to 320 m). The second site was within the Bahuaja Sonene National Park and the Tambopata Reserve Zone along the Tambopata River and near the Malinowsky guard post (12°30' to 13°01' S and 69°25' to 69°30' W, elevation 200 to 250 m). Mean annual rainfall in the region is between 2500 and 3500 mm with a marked dry season from June to September. Most precipitation falls during the months from December through February and the mean annual temperature is 24°C with a range from 10 to 38°C.

The vegetation at both sites is mostly pristine lowland Amazonian moist forest with three distinct vegetation types: *terra firme* forests, floodplain forest and palm swamps (aguajales) dominated by the palm *Mauritia flexuosa*. The floodplain forest is partly

inundated during the rainy season from December to March but there was little inundation during the time of the surveys. Mineral licks are common at Los Amigos, occurring at 11 sites within the study area and many more sites in other areas of the Los Amigos River watershed. At the Tambopata site we know of one lick within the study area and about three more in the surrounding area. All licks are located in the floodplain. Both sites have an extensive trail network that was used for this study.

Materials and Methods

Camera Traps

We carried out four camera trap surveys, three at Los Amigos and one at Tambopata (Table 4). We used Deercam (NonTipical Inc.) 35mm film passive infrared cameras operating 24 hours a day. The delay between pictures was set to 5 to 10 minutes and the sensitivity was set to high. Cameras were checked every five to six days to replace film and batteries if needed. All cameras were set on existing trails with a camera station consisting of two cameras facing each other, one on each side of the trail. Cameras were set in a regular grid with two kilometers between stations and an area in the center with 1 km camera spacing (except for the Los Amigos 2005 survey where the 1 km area was missing). The total area covered at Los Amigos was approximately 50 km^2 and at Tambopata 65 km^2.

Table 4: Dates and number of camera stations for four camera trap surveys carried out at two sites in Madre de Dios, Peru.

			Camera	Camera Stations		
Site	Dates	Days	Days	Floodplain	*Terra Firme*	Total
Los Amigos	14 Sept. - 13Nov. 2005	60	1440	8	16	24
Los Amigos	16 Aug. - 15 Oct. 2006	60	2400	14	26	40
Los Amigos	7 Sept - 5 Nov. 2007	60	2400	14	26	40
Tambopata	7 April – 7 June 2007	60	2580	20	23	43

To study the use of mineral licks by different ungulate species, we set camera traps at five mineral licks in the Los Amigos area during 2005 and 2006. For the licks we used Cuddeback (NonTipical Inc.) digital cameras. The delay was set to 5 minutes and sensitivity was set to high.

Data Analysis

Images from all surveys were scanned and entered into Camera Base (Tobler 2007) for data management and analysis. For all analyses, we defined the minimum time between two independent events as one hour. This means that if the same species was photographed more than once by the same camera in the course of one hour, this was only counted as one event.

Capture frequencies (event per 1000 camera days) and activity patterns were directly calculated by Camera Base. Photos taken half an hour before and half an hour after sunrise and sunset were classified as crepuscular (Gómez *et al.* 2005). Species with more than 80% of photos taken during the day were classified as diurnal, species with more than 80% of all photos taken at night as nocturnal and all other species as cathemeral.

To investigate habitat preferences for the different species we looked at difference in occupancy rates in *terra firme* and floodplain forests. Since the identification of individuals for ungulates is very difficult, the estimation of abundance using capture-recapture models used in camera trap surveys of large cats (Karanth and Nichols 1998; Silver *et al.* 2004) was not possible. Raw count data on the other hand are often a poor index for relative abundance in surveys where detection probability is <1 (Gibbs 2000). One possible solution is to use occupancy as a replacement for abundance (MacKenzie and Nichols 2004). MacKenzie *et al.* (2002) developed a model to estimate site occupancy and detection probability based on repeated presence-absence data from multiple sites. Royle and Nichols (2003) extended this model to allow for abundance-induced heterogeneity. The idea behind the Rolye-Nichols (RN) model is that site-specific detection probabilities vary due to differences in the number of individuals present at each site, and using a mixture model these abundances can be modeled based

on repeated presence-absence data. In the RN model, the occupancy Ψ is not directly estimated and has to be derived from λ, the average number of individuals at each site as $\Psi = 1 - e^{-\lambda}$. In simulations this model significantly improved occupancy estimates for data with high levels of heterogeneity (Dorazio 2007).The RN model assumes that populations are closed and that individuals are distributed in spaces according to a Poisson process. If these assumptions are violated, the estimated parameters should not be interpreted as abundance but rather as a random effect (MacKenzie *et al.* 2006:141). However, occupancy estimates will still be less biased than under models that don't include heterogeneity.

Preliminary data analysis confirmed that our camera trap data had a high level of heterogeneity which led us to use the RN model for all data analysis. The data was divided into ten sampling periods of six days each. This was necessary in order to increase the detection probability for each sampling period. Three possible covariates were used: Habitat (*terra firme* or floodplain), Site (Los Amigos or Tambopata) and Survey (Los Amigos 2005, Los Amigos 2006, Los Amigos 2007, Tambopata 2007), as well as their interactions. Models were ranked based on the Akaike information criterion (ACI) with the lowest value of ACI indicating the most parsimonious model (Burnham and Anderson 1998). All analyses were carried out in Presence (Hines 2007).

Results

Capture Frequencies and Habitat Use

Average capture frequencies for all surveys ranged from 13.2 for the red brocket deer to 59.6 for the white lipped peccary (Table 5). Frequencies differed greatly between the two habitats for grey brocket deer, which show a clear preference for *terra firme* forests. Capture frequencies were also higher for white-lipped peccaries in floodplain forest, but did not differ much between habitats for any of the other species. The results from the occupancy analysis confirmed these findings (Table 6, Table 7). All of the highest ranking models for the grey brocket deer included Habitat as a covariate. Occupancy for *terra firme* forest was much higher than for floodplain forests (0.505 vs 0.063). For the

red brocket deer the covariate Site was present in all models and occupancy was 20 percent higher for Tambopata compared to Los Amigos. None of the covariates were included in the top ranking model for the collared peccary, indicating no preference. Occupancy for that species was 0.691. For the white-lipped peccary both Survey and Habitat, as well as an interaction term, were included in the highest ranking model. This indicates that habitat use varied between different surveys. While for LA 05 and LA 07 there was little difference between the two forest types, white-lipped peccaries were using more of the floodplain forest for the surveys LA 06 and TA 07. For tapirs both site and survey were included, indicating a difference in occupancy between sites and a difference in detection probability between surveys, but no habitat preference.

Table 5: Capture frequencies expressed as number of photos / 1000 camera days for five ungulate species in the Peruvian Amazon.

Species	Survey	FP Freq	TF Freq	Both Freq (N)
Grey brocket deer	Los Amigos 2005	2.1	16.7	11.8 (17)
	Los Amigos 2006	0.0	23.1	15.0 (36)
	Los Amigos 2007	0.0	25.0	16.3 (39)
	Tambopata 2007	3.3	71.0	39.5 (102)
	All	1.5	34.6	22.0 (194)
Red brocket deer	Los Amigos 2005	8.3	4.2	5.6 (8)
	Los Amigos 2006	19.0	10.3	13.3 (32)
	Los Amigos 2007	9.5	11.5	10.8 (26)
	Tambopata 2007	16.7	21.7	19.4 (50)
	All	14.3	12.5	13.2 (68)
Collared peccary	Los Amigos 2005	4.2	21.9	16.0 (23)
	Los Amigos 2006	7.1	11.5	10.0 (24)
	Los Amigos 2007	19.0	18.6	18.8 (45)
	Tambopata 2007	25.8	11.6	18.2 (47)
	All	16.4	15.4	15.8 (139)
White-lipped peccary	Los Amigos 2005	66.7	65.6	66.0 (95)
	Los Amigos 2006	81.0	35.3	51.3 (123)
	Los Amigos 2007	102.4	71.8	82.5 (198)
	Tambopata 2007	67.5	21.0	42.6 (110)
	All	79.5	47.4	59.6 (526)
Lowland tapir	Los Amigos 2005	33.3	24.0	27.1 (39)
	Los Amigos 2006	29.8	25.6	27.1 (65)
	Los Amigos 2007	46.4	41.0	42.9 (103)
	Tambopata 2007	40.0	42.8	41.5 (107)
	All	38.1	34.1	35.6 (314)

TF: *terra firme*, FP: floodplain.

Table 6: Summary of model selection for the Royle-Nichols model for five Amazonian ungulate species.

Species	Model	AIC	ΔAIC[a]	*w*	N Par	-2l
Grey brocket deer	λ(Habitat) r(Site)	570.41	0.00	0.490	4	562.4
	λ(Habitat + Site) r(Site)	571.62	1.21	0.268	5	561.6
	λ(Habitat + Site) r(.)	573.12	2.71	0.126	4	565.1
Red brocket deer	λ(Site) r(.)	688.63	0.00	0.260	3	682.6
	λ(Site + Habitat) r(.)	690.48	1.85	0.103	4	682.5
	λ(.) r(Site)	690.64	2.01	0.095	3	684.6
Collared peccary	λ(.) r(.)	810.19	0.00	0.332	2	806.2
	λ(Habitat) r(.)	811.22	1.03	0.198	3	805.2
	λ(Site) r(.)	812.19	2.00	0.122	3	806.2
White-lipped peccary	λ(Survey * Habitat) r(.)	1523.33	0.00	0.513	9	1505.3
	λ(.) r(Survey*Habitat)	1524.52	1.19	0.283	9	1506.5
	λ(Site*Habitat) r(.)	1525.48	2.15	0.145	5	1515.5
	λ(Survey+Habitat) r(.)	1525.77	2.44	0.152	6	1513.8
Tapir	λ(Site) r(Survey)	1294.17	0.00	0.385	6	1282.2
	λ(Site + Habitat) r(Survey)	1296.15	1.98	0.143	7	1282.1
	λ(.) r(Survey)	1296.67	2.50	0.110	5	1286.7
	λ(Site) r(.)	1296.72	2.55	0.108	3	1290.7

Only models with a weight >0.1 are shown. [a]ΔAIC is the difference in AIC values between each model and the best model and *w* is the AIC model weight, NPar is the number of parameters and -2l is twice the negative log-likelihood.

Table 7: Occupancy estimates (Ψ) for five Amazonian ungulate species based on camera trap data. Estimates were made using the Royle-Nichols model.

Species	Habitat	Site/Survey	Ψ (SE)	95% confidence interval
Grey brocket deer	TF	all	0.505 (0.0649)	0.481 - 0.745
	FP	all	0.063 (0.0355)	0.033 - 0.280
Red brocket deer	all	LA	0.572 (0.1127)	0.505 - 0.907
	all	TA	0.812 (0.1045)	0.740 - 0.993
Collared peccary	all	Both	0.691 (0.0811)	0.656 - 0.923
White-lipped peccary	TF	LA 05	0.941 (0.0413)	0.919 - 0.999
	FP	LA 05	0.907 (0.0753)	0.849 - 0.999
	TF	LA 06	0.736 (0.0894)	0.690 - 0.958
	FP	LA 06	0.924 (0.0531)	0.892 - 0.998
	TF	LA 07	0.925 (0.0405)	0.908 - 0.996
	FP	LA 07	0.969 (0.0266)	0.954 - 1.000
	TF	TA 07	0.559 (0.1129)	0.492 - 0.900
	FP	TA 07	0.927 (0.0457)	0.904 - 0.998
Tapir	all	LA	0.795 (0.0645)	0.770 - 0.959
	all	TA	0.984 (0.0346)	0.912 - 1.000

TF: *terra firme*, FP: floodplain, LA: Los Amigos, TA: Tambopata.

Activity Patterns

The activity data shows that the two peccary species and the grey brocket deer are strictly diurnal, red brocket deer are active day and night and tapirs are mostly nocturnal with some occasional activity during the day (Table 8). The activity graphs (Figure 7) show that grey brocket deer and white lipped peccary are continuously active throughout the day from 6:00 until 18:00, while collared peccaries seem to have an activity peak in the early morning and are less active in the late morning and late afternoon. Red brocket deer have two activity peaks, one in the late afternoon after 16:00 and in the morning before sunrise; they mostly rest during the day between 10:00 and 16:00. Tapirs are active all night from 18:00 until 6:00 and show some activity in the early morning and late afternoon.

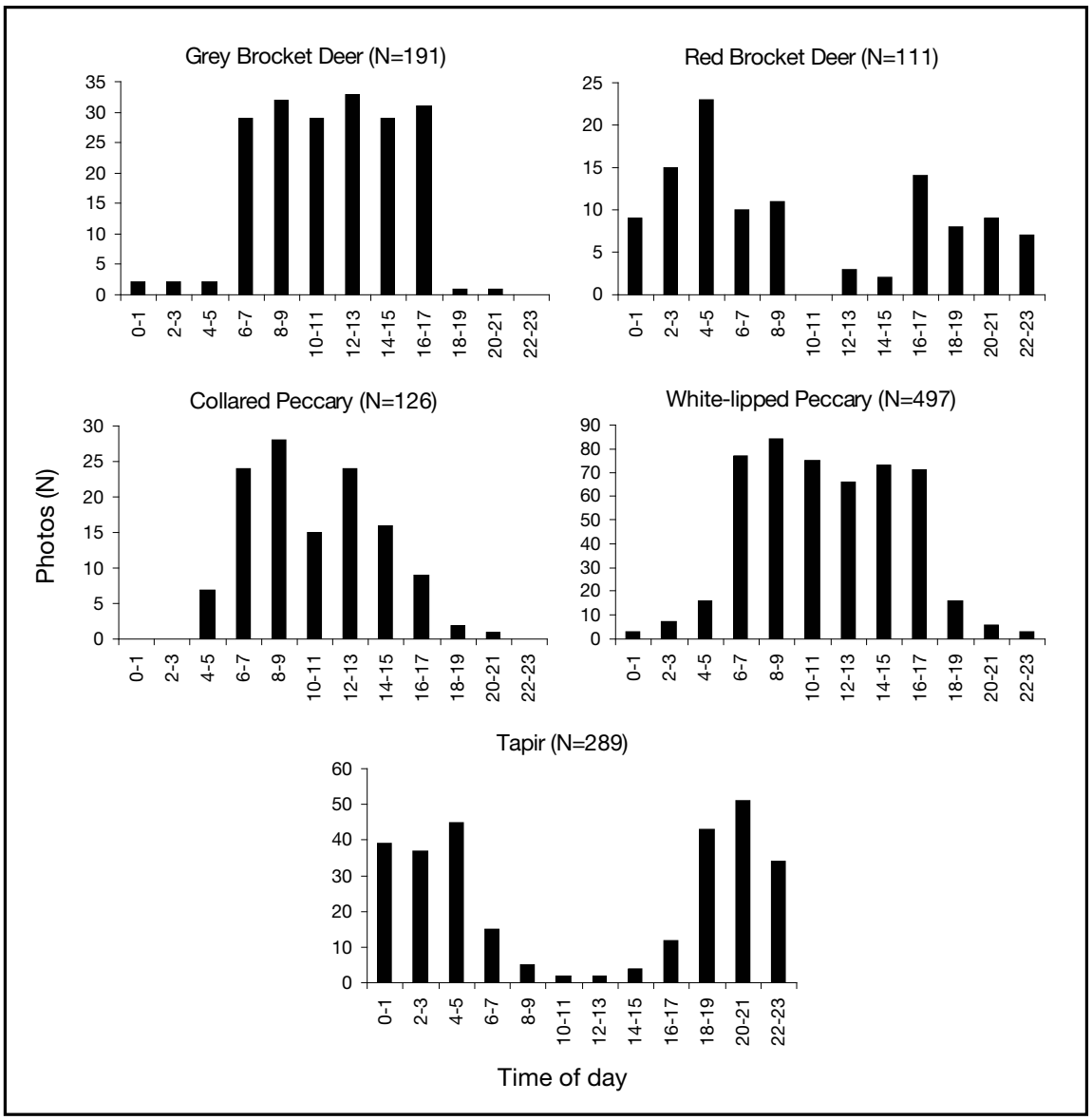

Figure 7: Activity patterns for five species of ungulates based on camera trap photos from the Peruvian Amazon. The total number of photos is indicated in parenthesis.

Table 8: Activity patterns for five species of ungulates based on camera trap photos from the Peruvian Amazon.

Species	N	Day	Night	Crepuscular	Classification
Grey brocket deer	191	90%	4%	7%	Diurnal
Red brocket deer	111	30%	51%	19%	Cathemeral
Collared peccary	126	90%	3%	6%	Diurnal
White-lipped peccary	497	86%	8%	6%	Diurnal
Tapir	289	10%	81%	9%	mostly Nocturnal

Use of Mineral Licks

There were clear differences in the use of mineral licks between the five species (Table 9). Tapirs were the most frequent visitors at all licks with an average visitation rate of 52.8 visits / 100 days (range 31.8-187.5). White-lipped peccaries and red brocket deer had a similar frequency of 16.1 (range 7.7-24.2) and 17.1 (range 4.6-52.9) respectively. Collared peccaries were only observed on three occasions during 434 camera days, and grey brocket deer were never seen at any of the licks.

Discussion

Habitat Use

The definition of habitat use is slightly different for the five species. The two habitats considered in this study, *terra firme* and floodplain forest occur in large, continuous areas. For all species with relatively small home ranges (brocket deer, tapir and most likely collared peccaries), this means that most individuals have their home range exclusively in either of the two habitat types and do not choose among habitats for their daily activities. Habitat use for these species is equal to difference in abundance in the two habitat types and we don't expect seasonal variations. The situation is different for white-lipped peccaries, which range over large areas and can easily move between the two forest types (Fragoso 1998). For white-lipped peccaries habitat use actually describes the proportion of use of the two habitats and can possibly vary throughout the year.

Table 9: Visitation frequencies of Amazonian ungulates at five different mineral licks in the Los Amigos Conservation Concession, Peru.

			Grey brocket deer		Red brocket deer		Collared peccary		White-lipped peccary		Tapir	
Lick	Date	Days	Freq	N	Freq	N	Freq	N	Freq	N	Freq	N
Hernan	24 April – 16 May 2005	22	-	-	13.6	3	-	-	27.3	6	68.2	15
Chica	24 April – 16 May 2005	22	-	-	4.6	1	-	-	13.6	3	31.8	7
Sarita	24 April – 20 May 2005	26	-	-	15.4	4	3.85	1	7.7	2	42.3	11
Hernan	10 June – 10 Oct. 2006	122	-	-	12.3	15	-	-	18	22	63.1	77
Chica	10 June – 10 Oct. 2006	122	-	-	17.2	21	0.82	1	16.4	20	43.4	53
Sarita	10 June – 11 Aug. 2006	62	-	-	14.5	9	1.61	1	24.2	15	33.9	21
Lago	10 Oct. - 03 Nov. 2006	24	-	-	12.5	3	-	-	8.3	2	187.5	45
CM3 Rio	12 July – 15 Aug. 2006	34	-	-	52.9	18	-	-	-	-	-	-
Total		**434**	**-**	**-**	**17.1**	**74**	**0.69**	**3**	**16.1**	**70**	**52.8**	**229**

Frequencies are expressed as number of visits per 100 days.

The only species showing a clear habitat preference was the grey brocket deer. Only five out of 189 photos for this species were taken in floodplain forests, indicating that grey brocket deer almost exclusively inhabit *terra firme* forests. Bodmer (1990b, Table 1) found that both brocket deer species prefer *terra firme* forests but other data showed that grey brocket deer preferred dryer habitats than red brocket deer (Bodmer 1991a). Data from other sites in the Amazon indicate that red brocket deer are more common than grey brocket deer (Hurtado-Gonzales and Bodmer 2004; Gómez *et al.* 2005). However, it is not clear if this holds for both *terra firme* and floodplain forest. Occupancy rates in our study for red brocket deer in *terra firme* forest were higher at both sites but only significantly higher for the Tambopata site. To our knowledge no other data exists on habitat preference of brocket deer in the Amazon.

While several authors showed that collared peccaries have a preference for *terra firme* forests (Bodmer 1990b; Peres 1996; Fragoso 1999), this was not confirmed by our data. Collared peccaries showed no clear preference for either forest type and were photographed more in floodplain forest in Tambopata. A possible explanation for this difference is that the floodplain forests in our study areas are only partly flooded and only for a few months out of the year, while in other parts of the Amazon they can flood for much longer periods of time.

White-lipped peccaries showed a preference for floodplain forests in half of the surveys and no preference in the other half. Since white-lipped peccaries can move over large distances, this is most likely caused by temporal differences in habitat use. White-lipped peccaries are often found in floodplain forests at the end of the dry season, feeding on the fruits of various palm species. The high overall occupancy values can be explained by the high mobility of the species. Occupancy in this case should be interpreted as use, and the results show that white-lipped peccaries use almost all of the forest during a two-month period.

Tapirs show no preference for either of the two forest types and are common throughout the forest occupying 80-100% of the area. Tapirs are often associated with swamps and riparian vegetation (Emmons and Feer 1997), but it seems that they are equally abundant

in *terra firme* forests. Telemetry data from Los Amigos showed that tapirs can have their home range exclusively in *terra firme* forests (Chapter VI).

Activity Patterns

Of the five ungulate species studied, three were diurnal, one cathemeral and one mostly nocturnal. This largely agrees with results found in the Madidi National Park in Bolivia (Gómez *et al.* 2005). The two peccary species show no difference in activity patterns, while the two brocket deer species have only little overlap in activity in the morning and late afternoon. Rivero et al. (2004) also found a clear difference in the activity patterns for brocket deer in the Bolivian Chaco, with red brocket deer being active mostly at night and grey brocket deer being active in the early morning. Data for three sites in the Chaco-Chiquitanía habitat in Bolivia show that grey brocket deer are largely diurnal (Maffei *et al.* 2002). In the Madidi National Park red brocket deer were more active at night and dawn than during the day (Gómez *et al.* 2005). The activity data for tapirs are in accordance with the data obtained with GPS collars from various individuals at Los Amigos (Chapter VI), indicating that camera traps collect reliable and unbiased activity data. Activity patterns at licks were almost identical with the data from the trails with white-lipped peccaries entering exclusively during the day, tapirs mostly at night and red brocket deer during day and night (Tobler unpublished data).

Use of Mineral Licks

Mineral licks are an important resource for at least three of the five Amazonian ungulate species. The use of mineral licks or more generally geophagy, the ingestion of soil, has been described for a large number of species of herbivore around the world, and in the case of large mammals, it has mostly been explained as mineral supplementation (Jones and Hanson 1985; Kreulen 1985; Holdo *et al.* 2002; Mills and Milewski 2007). Several studies showed that sodium is the main element sought by animals visiting licks (Tankersley and Gasaway 1983; Stark 1986; Moe 1993; Tracy and Mcnaughton 1995; Holdo *et al.* 2002), but other elements found in elevated concentration in lick soils are calcium, magnesium and potassium (Emmons and Stark 1979; Jones and Hanson 1985;

Klaus 1998; Montenegro 2004). Montenegro (2004) analyzed tapir diet in northern Peru and showed that sodium requirements cannot be met through the browse and fruits tapirs eat. She suggests that tapirs in that region therefore depend on sodium from mineral licks. Her data also showed that fruits have a much lower concentration of sodium than browse. Considering that peccaries and deer are largely frugivores (Bodmer 1991a), we would expect a similar or even higher deficiency for all species.

Tapirs were by far the most frequent visitors of mineral licks, followed by white-lipped peccaries and red brocket deer. The data also show that there are large differences between licks, indicating that certain species prefer some licks over others. Data from the Pantanal of Brazil show similar patterns with white-lipped peccaries being the most frequent visitors followed by tapirs (Pfeifer Coelho 2006). Visits by collared peccaries were actually more frequent than visits by brocket deer in that area.

All known licks in they Los Amigos River watershed occur in the floodplain forest. Therefore, animals with home ranges in the *terra firme* forest have to travel long distances to visit licks. Recent data from a telemetry study showed that tapirs may walk over 10 km to visit a mineral lick (Chapter VI) and white lipped peccaries usually include floodplain forests with licks in their home range area (G. Powell, pers. com.). Whether red brocket deer and collared peccaries also show long-distance travel to licks is currently unconfirmed.

We have no clear explanation why grey brocket deer and collared peccaries in our study area do not seem to be using licks, nor how they cope with mineral deficiencies. Grey brocket deer have been reported to visit licks in the Bolivian Chaco (Maffei *et al.* 2002) and in the Pantanal of Brazil (Pfeifer Coelho 2006) but were not found in two other studies in the Peruvian Amazon (Montenegro 1999; Montenegro 2004). One possible explanation is that all the licks surveyed were too far away from the *terra firme* to be visited by grey brocket deer, which almost exclusively inhabit *terra firme* forests. However, the same explanation cannot be used for collared peccaries, which are similarly abundant in both forest types.

While mineral licks are important resources for ungulates, they are at the same time well-known places for local hunters and hunting at licks is often the preferred method for hunting tapirs (Montenegro 2004; pers. obs.). Considering that licks are visited by a large number of individuals from the whole populations surrounding the lick, the potential impact of hunting at licks can be high. It is therefore important to give special attention to mineral licks when developing conservation or management plans for ungulate populations.

Resource Partitioning

Resource partitioning among Amazonian ungulates was first studied by Bodmer (1991a) in northern Peru. He analized at diet and habitat use and concluded that each species partitioned at least one resource type from every other species. Red brocket deer differed from grey brocket deer in their use of habitat and the same was true for collared and white-lipped peccaries. Red brocket deer and collared peccaries used similar habitats but differed in their diet. Tapirs differed from all other species in their diet.

Bodmer's (1991a) data showed that the closely related species have a very similar diet and therefore resource partitioning would have to occur at the spatial level for these species. In our study area the grey brocket deer was the only species that was almost completely restricted to *terra firme* forest. The white-lipped peccary showed a preference for floodplain forests but was also common in *terra firme* forests. All other species were equally common in both habitat types. Over 25 percent of all cameras recorded four of the five species and overlap would probably be even larger were detection probabilities considered.

If we assumed a high competition between grey and red brocket deer due to their similar diets, we would expect red brocket deer to be more common in floodplain forest where grey brocket deer are absent. This however is not supported by our data. It is possible that resource partitioning occurs on a temporal scale instead, with the grey brocket deer being mostly active during the day and the red brocket deer during the night.

Collared peccaries and white-lipped peccaries share the same activity patterns and are common in both habitat types. Resource partitioning might take place on the scale at which these two species use the landscape as suggested by Fragoso (1999). Collared peccaries exploit dispersed resources on a small scale and white-lipped peccaries moving between large patches of resources (e.g. palms) dispersed throughout the landscape (Kiltie and Terborgh 1983; Fragoso 1999).

Tapirs are common throughout the study areas. Tapirs have a diet that includes much more browse than the diet of the other ungulates (Bodmer 1991a). Therefore, resource partitioning most likely takes place at the diet level. However, tapirs can still compete with other ungulates for fruits, which compose an important part of their diet (Chapter IV). They mostly nocturnal and therefore only share their activity period with the red brocket deer.

Conclusions

Our results show that camera traps have a great potential for rapidly increasing our knowledge of the distribution, relative abundance, habitat use and activity patterns of large rainforest mammals. Camera traps can also give detailed information on the use of resources such as mineral licks, water holes or fruit patches by different mammal species. Once the equipment is purchased, surveys can be carried out at relatively low costs and in short time periods. Much of these data could otherwise only be collected by radio telemetry, which is logistically much more difficult and expensive. Based on our own experience and the results from other studies (Maffei *et al.* 2002; Gómez *et al.* 2005), we believe that camera traps are the most efficient tool available for assessing activity patterns of large cryptic rainforest mammals. Unlike capture-recapture models, activity patterns rely on almost no assumptions. Data can come from a large number of individuals or from repeated photos of a few individuals, as long as events are independent. In addition data from several surveys can be pooled. Camera traps also have the advantage that they allow analysis of activity patterns at the population level, where data comes from many different individuals; whereas telemetry studies often

collect data from only a few individuals. Data on habitat use collected with camera traps will never replace telemetry studies for detailed habitat studies but can establish important knowledge about the distribution of several species within a study area. Seasonal differences can be attained by conducting surveys at different times of the year.

With occupancy models, new approaches are emerging for analyzing repeated presence absence data for relative abundance and habitat use of species with no individual markings (Stanley and Royle 2005; MacKenzie *et al.* 2006). These applications still need further testing for practical applications and are currently not widely used in camera trap studies, but they show great potential for gaining additional knowledge from existing and newly generated camera trap data.

CHAPTER IV
FRUGIVORY OF LOWLAND TAPIRS IN THE PERUVIAN AMAZON

Synopsis

Fruit consumption of lowland tapirs in the southwestern Amazon was studied by examining seeds from 135 dung samples collected between 2005 and 2007. A total of 122 species of seeds, representing 68 genera and 33 families, were identified. The species accumulation curve showed that more species can be expected with further sampling. Most species (45%) were only encountered once, and only 10% of all species were found in more than 10 samples, indicating that tapirs are opportunistic foragers. The most frequently encountered species was *Mauritia flexuosa* (Arecaceae) followed by an unidentified Bombacaceae species, *Ficus sp. (Moraceae)*, *Perbea sp. (Moraceae)* and *Genipa americana (Rubiaceae)*. *Ficus* was the most frequent and diverse genus encountered in the fecal samples.

Seed diversity showed a clear seasonal pattern and was highly correlated with fruit availability. The most diverse months were February and November, the fewest species were found from June to August during the dry season.

Seeds width ranged from <1 mm to 25 mm. Eighty-one percent of all species consumed by tapirs were <10 mm in width and species of size class 15-20 mm and 20-25 mm only showed up in 6 and 14% of all samples respectively. The size distribution of seeds found in tapir feces generally followed the size distribution of seeds found in the forest with a somewhat lower proportion of seeds found in the smallest size class <2.5 mm and more seed found in the largest size class 20-25 mm.

The diversity of seeds found in tapir dung in this study was much higher than in other studies. The large number of small seeds showed that tapirs compete for fruits with other frugivores such as brocket deer and peccaries. They are potential dispersers for a large number of species, some of which are probably dispersed only by large primates and tapirs.

Introduction

Lowland tapirs (*Tapirus terrestris*) are the largest terrestrial mammal in South America and occur from Colombia to northern Argentina in a wide range of ecosystems including tropical moist forests, xeric Chaco and Cerrado forest, savanna wetlands and lower montane forests (Bodmer 1990b; Taber *et al.* 2006). As hindgut fermenters they satisfy their nutritional requirements by processing large quantities of low-quality browse (Foose 1982). Tapirs have a broad diet, feeding on a wide variety of plants but at the same time they selectively choose among available species (Terwilliger 1978; Janzen 1982b; Williams 1984; Bodmer 1991a; Naranjo 1995a; Salas and Fuller 1996; Montenegro 2004). While their main diet consists of browse, they consume fruit extensively when available (Bodmer 1990a; Fragoso 1997; Foerster and Vaughan 2002). It has been suggested that tapirs consume fibrous vegetation for protein and depend on more digestible foliage and fruit for energy (Foose 1982). Over 150 species of fruits in 51 different families have so far been identified to be eaten by the lowland tapir throughout its range (Bodmer 1991a; Rodrigues *et al.* 1993; Salas and Fuller 1996; Olmos 1997; Fragoso and Huffman 2000; Galetti *et al.* 2001; Tófoli 2006). However, the importance of fruit in the tapir's diet seems to vary between study sites. Bodmer (1990a) showed that the diet of lowland tapirs in a lowland tropical rainforest in Peru can consist up to 33% of fruit. Henry et. al. (2000) found a range of 15 to 36% for French Guiana. In Baird's tapir (*Tapirus bairdii*) varied between 3.2-12% for fecal analysis (Naranjo 1995a) and 12.4-22.3% for direct observations (Foerster 1998). Naranjo and Cruz (1998) found fruits to make up 6.2-8.1 % of the diet of the same species in several forest types from lowland moist forest to montane forests in Chiapas, Mexico. The proportion of fruit consumed can vary strongly between dry and wet seasons (Naranjo 1995a; Foerster 1998; Naranjo and Cruz 1998; Henry *et al.* 2000), which is most likely related to the large seasonal difference in fruit availability in many tropical forests (Altrichter *et al.* 2001).

Tapirs are the only large terrestrial mammal in the neotropical lowlands that regularly ingests a wide range of intact seeds, while most other species mainly act as seed

predators (Bodmer 1991a). Many authors suggested that lowland tapirs therefore play an important role as long-distance seed dispersers, transporting seeds over distances of several kilometers and dropping viable seeds with their feces (Bodmer 1991a; Rodrigues *et al.* 1993; Fragoso 1997; Henry *et al.* 2000; Galetti *et al.* 2001; Fragoso *et al.* 2003). Fragoso et al. (2003) showed how tapirs influence the reproductive success and distribution of the palm *Maximiliana maripa* by dispersing seeds away from mother plants where they would be infested and killed by bruchid beetles. However, the efficiency of tapirs as seed dispersers is still under debate. Janzen (1981) found that the Baird's tapir was an effective seed predator for two tree species in Guanacaste, Costa Rica and Salas and Fuller (1996) argued that tapir's preference to defecate in water places seeds in unsuitable locations for germination.

In this paper we present an analysis of the diet of lowland tapirs in the southwestern Amazon. We look at seasonal variation in fruit consumption and correlated that with the abundance and the phenology of trees in the region. We quantify seasonal variation in fruit consumption and correlate it with plant diversity and phenology in the region. We evaluate the tapir's preference for fruits from certain groups of plants and look at the diversity and size distribution of seeds found in tapir feces. Lastly, we discuss the possibility of tapirs being efficient seed dispersers.

Study Area

This study was carried out in the Los Amigos Conservation Concession (12°30' to 12°36' S and 70°02' to 70°09' W, elevation 250 to 320 m), a 1400 km^2 privately managed protected area in the department of Madre de Dios, Peru. The climate is tropical with a marked dry season from June to September and a rainy season during the months of November through April. Mean annual rainfall is between 2500 and 3500 mm and the mean annual temperature is 24°C with a range from 10 to 38°C.

The area is covered by continuous, mostly primary lowland Amazonian moist forest, and three major vegetation types can be distinguished in the study area: (1) *terra firme* forests, (2) floodplain forests, and (3) wetlands. Terra firme forests exist on the high and

often dissected terraces that are characteristic of the region. They consist of relatively poor soils, evident in the high root biomass visible on the surface of the forest floor, and they are dominated by tree species in the families Fabaceae, Sapotaceae, Lecythidaceae, Flacourtaceae, Annonaceae, Moraceae, Myristicaceae, and others. A complex network of small and large streams flowing to the Madre de Dios and Los Amigos Rivers has dissected the terra firme forests. The creeks formed have richer soils but they are often sloped, and they harbor many shrubs and small trees that can often be found in floodplain forest, as well as many species of Pteridophytes. Floodplain forests are often seasonally inundated, at least in low-lying areas, and consist of rich fluvial soils originating from the sediment-heavy Madre de Dios River and its tributary, the Los Amigos River. They are dominated by tree species in the Arecaceae, Annonaceae, Moraceae, Fabaceae, Bombacaceae, Myristicaceae, Euphorbiaceae, and others. Wetland vegetation consists of gradients and transitions between: (1) palm swamp forest dominated by *Mauritia flexuosa* (Arecaceae), (2) stunted swamp forest dominated by species of the Clusiaceae, Chloranthaceae, Melastomataceae, Rubiaceae, Myrtaceae, and Fabaceae, (3) bogs dominated by Pteridophytes, Cyperaceae, Poaceae, Juncaceae, Orchidaceae, and Lentibulariaceae, and (4) open-water oxbow lakes surrounded by floodplain forest, with occasional floating aquatic plants.

The Los Amigos Conservation Concession harbors an intact large mammal community including five species of ungulates, 14 species of carnivores, and 11 species of primates (Chapter II, pers. obs.). Tapirs are abundant in all habitat types and overlap with other terrestrial frugivores such as white-lipped peccaries (*Tayassu pecari*), collared peccaries (*Pecari tajacu*), red brocket deer (*Mazama americana*) and grey brocket deer (*Mazama gouazubira*) (Chapter III).

Materials and Methods

Sample Collection and Preparation

Tapir dung was collected between May 2005 and October 2007. We collected dung encountered while hiking the forest during research activities in the area as well as from

known latrines (sites where tapirs regularly defecate). Only dung that was found in intact piles and that was not more than a few days old, judged by its odor and color, was collected. Dung was washed in a sieve with mesh size of 0.5 mm while fresh and then dried either in the sun or in a plant drying oven (Bodmer 1990a; Fragoso and Huffman 2000; Galetti *et al.* 2001; Tobler 2002). It was then stored in plastic bags until processing.

Dung was separated into fruit parts and vegetative parts. All fruit parts were divided by species and all seeds were counted. In cases where there were thousands of small seeds of a single species (e.g. *Ficus spp.*) we would separate a small sub-sample, weigh it, count the seeds, and then use that to estimate the total number of seeds in the whole sample.

Vegetation Data

Vegetation data were collected as part of a large botanical inventory (Los Amigos Botany Program) conducted between 2001 and 2007 when an intensive collection program resulted in a fairly complete species inventory of the region. Forest composition was evaluated with 69 0.1 ha "Gentry"-transects units, each consisting of 10 parallel 2x50 m transects, distributed throughout the study area in both *terra firme* (40 units) and floodplain forests (29 unit). All stems >2.5 cm in diameter at breast height (DBH, 1.3 m) were recorded, but only stems larger or equal to 10 cm DBH were used for the analysis. Data on plant phenology was recorded based on 1520 marked plants belonging to 283 species in 210 genera. Each individual was visited monthly from May 2002 onward and the presence or absence of different reproductive parts (flowers, buds, immature fruits, mature fruits) was recorded. Starting in 2004 an index on a scale from one to five was used to quantify flower and fruit abundance.

Seed Identification

Seeds from all samples were compared and organized into morphospecies. All seeds were identified to family level, and to genus and species level if possible based on herbarium specimens and a seed collection from the area With the help of a seed guide

for the area currently in production (Cornejo and Janovec 2008), seed identification was enhanced by recent knowledge of seed morphologies and the availability of existing seed images representing the majority of the plant genera present in the region. Characters of size, form, color, texture, and pubescence were used in the comparison and identification of all seed collections. Identification to the family and genus level was achieved for the majority of the seed collections. However, identification to species is often difficult, if not impossible, and therefore morphospecies numbers were used for many of the seeds. Weight and size of each species was taken as an average from 3-5 seeds.

Data Analysis

To compare species diversity between months we standardized the sample size for all months to eight samples, which was the minimum of samples collected for all months except for December. We then used rarefaction techniques (Colwell and Coddington 1994) to estimate the expected number of species at the level of eight samples for months with a larger number of samples, and to calculate a rarefied species accumulation curve to evaluate the completeness of the species list. Rarefaction was done in EstimateS (Colwell 2006). In order to compare the seed diversity for each month with plant phenological data, we generated a fruit abundance index by taking the average of the quantitative measure for mature fruits for all animal dispersed species (239 species, 1195 individuals). This index takes into account both the diversity (the more species that have fruits the higher the average) as well as the fruit abundance (the higher the index for each individual the higher the average).

To look at the size distribution of seed ingested by tapirs we used seed width as a measure (Bodmer 1991b). We compared the observed distribution of seed size to the size distribution for 543 genera from the study area based on data from (Cornejo and Janovec 2008). The analysis was carried out at the generic level. For genera with multiple species the average width was used. Fruits of species in the same genus are usually morphologically very similar for plants in the study area (Janson 1983). We also looked at the frequency of occurrence for different size classes.

Results

We collected a total of 135 samples of tapir dung during the study period. Of these, 53% were found at tapir latrines and the rest were found at numerous locations throughout the study area. Seventy percent of all samples were found in water; this percentage was similar for latrines (75%) and samples encountered during walks (63%) (Chi^2=1.90, df=1, p>0.1). Seventy-six percent of all samples were found in *terra firme* forest where all latrines were located. Samples found by walking were found in floodplain and *terra firme* in equal numbers. The number of samples was unevenly distributed over the year with the monthly number of samples ranging from 6 to 25 (Table 10). Seeds made up 0 to 56% (mean=5.8%) of the dry weight with leaves and fibers accounting for the rest. We recorded a total of 122 seeds species in 68 genera and 33 families (Appendix B).

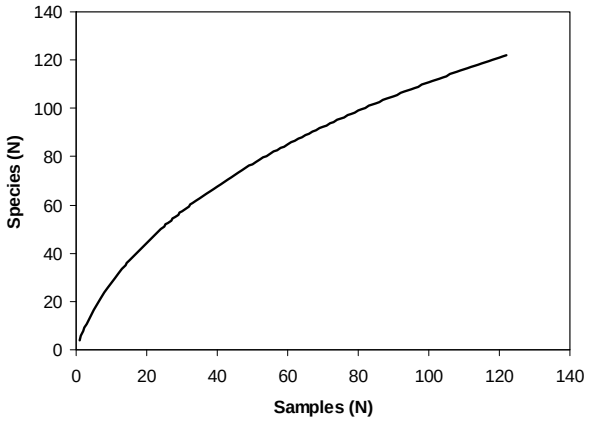

Figure 8: Species accumulation curve for seeds found in tapir dung samples in the Peruvian Amazon. The total number of samples was 135 and samples were collected during all months of the year.

The species accumulation curve clearly shows that many more species could be found with continued sampling (Figure 8). The frequency distribution for all species shows that 45% of all species were only encountered once, 81% in one to five samples and only 10% in more than 10 samples (Figure 9). Only 13 dung samples did not contain seeds. The majority of the seeds found were intact; however we did not test their viability.

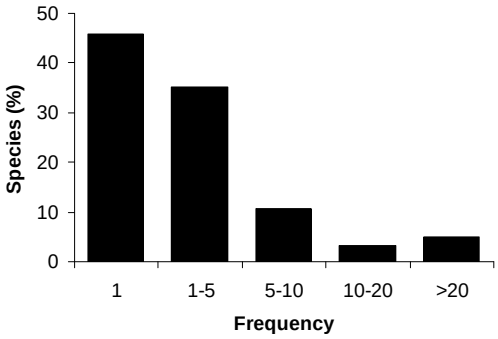

Figure 9: Frequency of occurrence distribution of 122 seed species found in 135 tapir dung samples.

Table 10: Number of tapir dung samples, number of seed species found and the Fruit Availability Index (FAI) for each month of the year.

		Seed Species					
Month	Samples	Total	Rarefied	Min	Max	Average	FAI
January	10	25	23	0	9	5.1	0.29
February	8	35	35	3	12	7.8	0.33
March	10	24	22	5	8	6.5	0.28
April	8	22	22	3	6	5.1	0.22
May	13	27	20	0	6	3.8	0.20
June	25	28	15	0	7	2.0	0.13
July	16	21	14	0	5	2.2	0.11
August	8	13	13	0	7	3.3	0.14
September	11	22	18	1	10	3.7	0.18
October	8	23	23	2	8	5.5	0.17
November	12	32	24	1	10	5.2	0.17
December	6	14	- *	1	6	3.2	0.18

For comparison purposes between months, rarefaction was used to estimate the expected number of species at a level of eight samples for all months with a higher number of samples. * The total number of samples for December was less than eight.

The most common families found in tapir dung were Moraceae, Arecaceae, Bombacaceae and Rubiaceae (Table 11). For Areaceae the high frequency was mostly caused by the species *Mauritia flexuosa*, which was found in 45 percent all samples. However, out of 62 samples that contained *Mauritia* remains, only eight samples contained seeds, all others only contained scales. The second most common species was

an unidentified species in the family of Bombacaceae followed by a species of *Ficus*, *Perebea*, *Genipa americana* and *Ocnychopetalum periquino*. At the genus level the genus *Ficus* was the most common after *Mauritia*, followed by *Perebea* and *Pouteria* (Table 12). *Ficus* was also the most diverse genus. The families with the most species were Moraceae, Rubiaceae and Annonaceae. Abundant families with fruits that are not or only very rarely eaten by tapirs are Myrisitcaceae, Lauraceae and Lecythidaceae.

While at the family level the frequency of occurrence was correlated with the abundance in the study area (Spearman's rho=0.690, $p<0.001$, N=27), this was not the case at the genus level (Spearman's rho=0.140, $p=0.35$, N=46).

Table 11: The most common families of seeds found in 135 tapir dung samples in the Peruvian Amazon.

Family	Genera	Species	Samples (N)	Samples (%)	Months	Density (N/ha)
Moraceae	5	22	82	61%	12	75.1
Arecaceae	4	5	71	53%	12	73.9
Bombacaceae	5	5	46	34%	12	25.7
Rubiaceae	5	18	39	29%	12	15.2
Annonaceae	8	12	36	27%	8	30.4
Sapotaceae	2	7	27	20%	7	57.4
Cecropiaceae	2	6	23	17%	11	50.1
Fabaceae	7	7	14	10%	6	80.9

Density is based on data from 69 0.1 ha forest transects from the study area and includes all tress with a diameter of 10 cm and more.

Table 12: The most common genera of seeds found in 135 tapir dung samples in the Peruvian Amazon.

Family	Genus	Species	Samples (N)	Samples (%)	Months	Density (N/ha)
Arecaceae	Mauritia	1	60	44%	12	0.3
Moraceae	Ficus	14	54	40%	12	3.6
Bombacaceae	Indet	1	38	28%	12	-
Moraceae	Perebea	5	33	24%	7	0.9
Sapotaceae	Pouteria	5	25	19%	7	31.0
Annonaceae	Onychopetalum	1	22	16%	5	1.0
Rubiaceae	Genipa	1	22	16%	10	0.4
Cecropiaceae	Cecropia	5	18	13%	9	6.8
Annonaceae	Duguetia	1	14	10%	6	1.0

Density is based on data from 69 0.1 ha forest transects from the study area and includes all tress with a diameter of 10 cm and more.

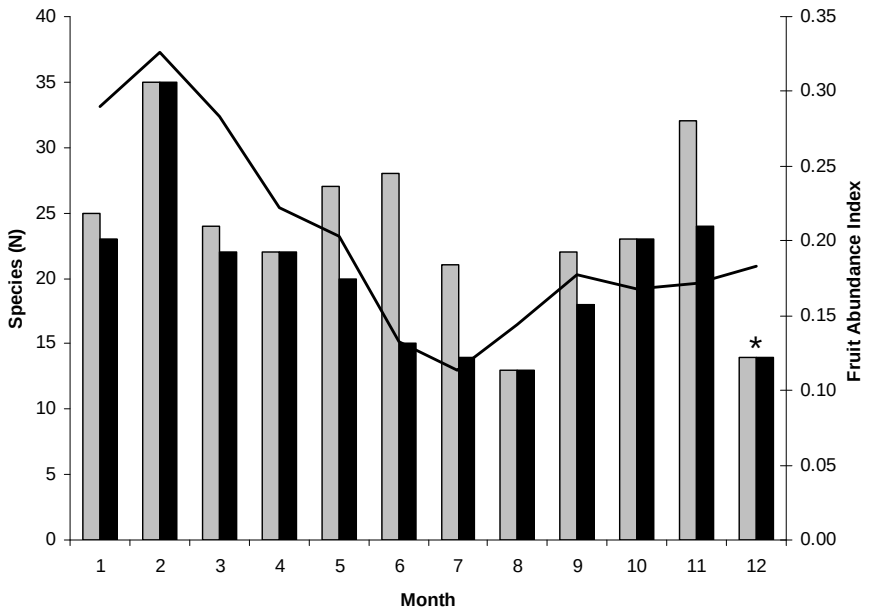

Figure 10: Monthly number of seed species found in tapir dung in the southwestern Amazon. Grey bars show the total number of species, black bars show the number of species rarefied to eight samples. The black line shows a fruit abundance index calculated from phenological data from 239 species and 1195 individual plants, which correlated well with the rarefied number of species (Spearman's rho=0.610, $p<0.05$, N=12). *Only 6 samples were found in December, the rarefied number is shown at the level of 6 samples.

The month with the highest seed diversity was February, with 35 species, followed by November with 32 species. Diversity shows a clear seasonal pattern that is related to plant phenology (Figure 10). Both the rarefied number of species per month as well as the average number of species per month are positively correlated with the fruit availability index (Spearman's rho=0.610, $p<0.05$, N=12 and Spearman's rho=0.692, $p<0.05$, N=12).

The range of seed sizes encountered was between <1 mm and 25 mm in width. No seeds wider than 25 mm were found. Seed weight ranged from 0.01 (the minimum of the balance used) to 7.7 g. The largest and heaviest seeds mostly came from palms of the species *Mauritia flexuosa, Astrocaryum murmuru, Oenocarpus mapora*, as well as from *Anomospermum reticulatum* (Menispermaceae). Width and weight were highly correlated (Spearman's rho=0.929, $p<0.001$, N=116) so that results shown for width apply equally to weight. The size distribution of different genera shows that seeds 5-10 mm in width are most diverse, followed by genera with seeds in the size class 2.5-5 mm (Figure 11a). Tapirs consume fewer genera of seed than expected in the size class 0-2.5 mm and more in the size classes 2.5-5 mm and 20-25 mm (G-test: G=14.33, df=6, $p<0.05$). 81% of all species were <10 mm. The smaller size classes from 0 to 10 mm are the most common ones, occurring in 50% of all samples while large seeds (>15 mm) only show up in 6-14% of all samples (Figure 11b). Frequency is highly correlated with species diversity in each size class (G-test: G=2.28, df=5, p=0.81) and somewhat less with generic diversity (G-test: G=5.45, df=5, p=0.36).

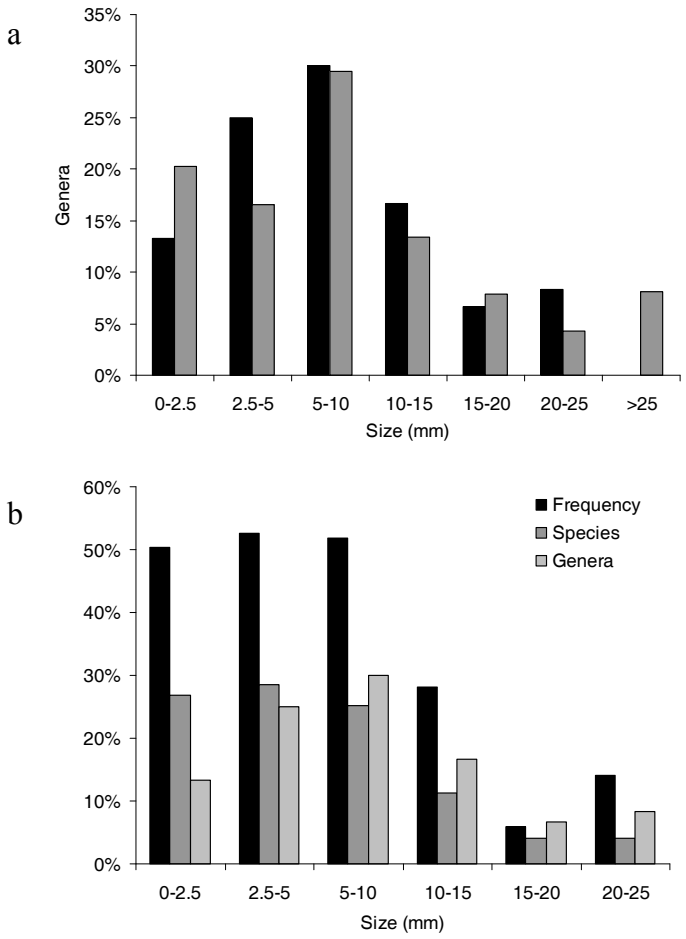

Figure 11: Size distribution of seed found in tapir dung in the Peruvian Amazon. a) The distribution of 68 genera found in tapir dung compared to the distribution of 543 representative genera from the same area. Black bars show seeds from tapir dung, gray bars seeds from the reference collection. b) The frequency of different seed size classes found in tapir dung and the number of species and genera found in the dung samples.

The number of seeds found in a sample is clearly related to the seed size (Table 13). There are three general classes: (1) seeds <2.5 mm which can appear in quantities of several thousands in a sample, (2) seeds between 2.5 and 15 mm in width where the average number ranges from 30 to several hundred seeds per sample, and (3) seeds >15 mm with few seeds on average and a maximum number of about 50 seeds per dung pile.

Table 13: Summary of the size distribution of seeds found in 135 tapir dung samples.

Seed Width	Diversity[a]		Frequency[b]	Abundance[c]	
(mm)	Genera	Species		Mean ± SD	Max
0-2.5	8	33	50%	5587 ± 21664	171766
2.5-5	15	35	53%	33 ± 77	439
5-10	18	31	52%	38 ± 94	499
10-15	10	14	28%	23 ± 44	236
15-20	4	5	6%	7 ± 12	37
20-15	5	5	14%	10 ± 15	52

[a] Total number of genera and species found in that size classs. [b] percentage of all samples that contained seeds of that size class. [c] Mean and maximum number of seeds found in a sample

Discussion

Fruit Consumption by Tapirs

The number of fruit species found to be consumed by tapirs in this study was three to ten times higher than in other studies with comparable sample sizes (Naranjo 1995b; Salas and Fuller 1996; Fragoso and Huffman 2000; Tófoli 2006). Only data from French Guiana showed a similar diversity (when corrected for sample size) with 42 species found in 27 stomach samples (Henry *et al.* 2000). While the most common species eaten by tapirs we certainly recorded in this study, the species accumulation curve indicates that the species list is far from complete. We estimate that there are over 200 species of fruits occasionally eaten by tapirs. Comparing our list to published results from other studies (Bodmer 1991a; Rodrigues *et al.* 1993; Salas and Fuller 1996; Olmos 1997; Fragoso and Huffman 2000; Galetti *et al.* 2001; Tófoli 2006) we found six new families and 47 new genera for the lowland tapir's diet.

Most species occurred in less than five samples, and almost half of the species only showed up in one sample. This indicates that tapirs consume fruits opportunistically, eating a wide variety of fruits encountered during their foraging activity. This is also supported by the clear correlation of the diversity of species consumed with fruit availability. The more fruit species that are available the greater the number of species

tapirs consume. At the family level the frequency of occurrence is clearly related to abundance, however this is not as clear on a genus and species level. Some species that are frequently eaten by tapirs are relatively rare and others that are abundant are rarely eaten. In some cases the low incidence of many species may be related to a short fruiting season for those species. Even if some species are abundant, their fruits are only available during a short period of time, and therefore only show up in a small number of samples.

Only ten species occurred in more than ten samples and might be actively sought after. The species that occurred with the highest frequency was *Mauritia flexuosa*, a species that usually grows in large patches in swamp areas in the floodplain forest and along stream beds in the *terra firme* forest. Telemetry data from the study area shows that tapirs actively seek out these patches for foraging, probably both on herbaceous plants and *Mauritia* fruits (Chapter VI). Active selection of *Mauritia* patches has also been documented for northern Peru (Bodmer 1990a; Montenegro 2004), and *Mauritia* was the most frequently consumed fruit in those studies, with 70-76% of occurrence, as well as in the northwestern Amazon with 70% of occurrence (Fragoso and Huffman 2000). It seems to be less important in French Guiana where it only occurred in 7% of all samples (Henry *et al.* 2000), but this could be related to the local abundance of the palm species.

Moraceae was the most important family occurring in over 60% of all samples, with *Ficus* and *Perebea* being the preferred genera. While Moraceae are generally abundant, the two genera preferred by tapirs only make up a small proportion of the trees in that family. However, many *Ficus* trees produce a large amount of fruit that is readily available to terrestrial frugivores. Two other families that occur with high frequencies and have a larger number of species eaten by tapirs are Rubiaceae and Annonaceae. Both of them produce large fleshy fruits. The same is true for the family Sapotaceae where the genus *Pouteria* was the most commonly eaten.

Our results clearly show that tapirs ingest mostly smaller seeds with a width < 10 mm. 68% of all species were found in that size class and 84% of all samples contained seeds <10 mm. Seeds >15 mm were found in less than 20% of all samples and only 15% of all

species were in that size class. Size class distribution followed the distribution of available size classes with somewhat less species <2.5 mm and more species in the classes 2.5-5 mm and 20-25 mm than expected. Tapirs don't seem to ingest seeds larger than 25 mm and it is possible that the low frequency of larger seeds is related to tapirs spitting them out, as has been repeatedly documented for *Mauritia flexuosa* seeds (Bodmer 1990a; Bodmer 1991b; Fragoso and Huffman 2000; Henry *et al.* 2000, this study). In French Guiana 60% of all species (N=40) were <10 mm (Henry *et al.* 2000). These findings contrast with results from northern Peru, where Bodmer (1991b) found that about 90% of all seeds ingested by tapirs were larger than 10 mm and 60% larger than 20 mm. The higher rate of consumption of smaller fruits could mean that dietary overlap and competition for fruits between tapirs and other Amazonian ungulates is more important then previously thought (Bodmer 1991b). Many genera and species found in this study are also consumed by both species of peccaries (Beck 2005). Although tapirs consume more browse than all other species and depend less on fruit, fruits represent a high energy component in their diet and habitats with high fruit abundance might support larger tapir populations. However, exactly how strong this relationship is remains to be shown.

Tapirs as Potential Seed Dispersers

Tapirs are potential dispersers for hundreds of plant species in many different plant groups and size classes. While species with small seeds are dispersed by a wide range of frugivores, large-seeded species often rely on a few large-bodied frugivores, mostly large primates of the genus *Ateles*, *Lagothrix* and *Alouatta* which are the only Neotropical primates that disperse seeds of 25-46 mm in length. (Peres and van Roosmalen 2002). In this study we found 18 plant genera listed by Peres and van Roosmalen (2002) as primarily or exclusively dispersed by large primates also to be dispersed by tapirs, indicating that tapirs can be an important long-distance disperser for many of these large-seeded species. The diversity of seeds dispersed by tapirs is comparable to that of large-bodied primates, that have been shown to disperse between

70 and 200 seed species (Andresen 1999; Stevenson 2000; Andresen 2002; Peres and van Roosmalen 2002).

The effectiveness of tapirs as seed dispersers depends on two factors: (1) the viability of seeds defecated by tapirs and (2) the post-dispersal fate of the seeds (Schupp 1993). A review of 80 studies including many plant and animal species showed that gut passage usually has no impact or a positive impact on germination success of seeds; in less than 20% of all studies negative impact was found (Traveset 1998). The same review also showed that effects can be highly variable for different species ingested by the same animal species, even for closely related species. Results for one species can not readily be applied to another. This is consistent with different studies on the impact of ingestion by tapirs on the viability of seeds, where results varied from negative to neutral and positive (Janzen 1981; Janzen 1982a; Williams 1984; Rodrigues *et al.* 1993; Fragoso 1997; Fragoso *et al.* 2003). But even if germination rates were reduced through gut passage, tapirs likely still defecate a large number of viable seeds from many species.

Whether a deposition site is suitable for seedling establishment or not depends largely on the plant species (Schupp 1993; Stevenson 2007). In our study area we found feces at latrines and scattered throughout the area in terra firma, floodplain and swamp forest. The proportion of feces found at latrines is not representative for the defecation behavior of tapirs. During more than three years of field work in the area we found only three latrines, and judging by the number of feces encountered each was probably used only by one or two individuals and with low frequency. This leads us to believe that tapirs defecate at a large number of sites throughout the area, with about 60% of all feces deposited in water and 40% at dry sites, supporting an argument by Fragoso and Huffman (2000) that tapirs deposit many seeds in safe places where they could germinate. Long gut retention times of 2-15 days results in defecation of seeds over a period of several days (Janzen 1981; Olmos *et al.* 1999) and home range sizes of 100 to 350 ha (Chapter VI) can result in a large seed shadows with seeds deposited at multiple sites.

Few studies have looked at post-dispersal fates of seeds dispersed by tapirs and most of them have focused on large palm seeds (Fragoso 1997; Olmos *et al.* 1999; Quiroga-Castro and Roldan 2001; Fragoso *et al.* 2003; Rios and Pacheco 2006). These studies showed that a combination of distance to parent trees and protection by dung greatly reduce the infection rate of seeds by parasitic insects and therefore increased survival and germination rates. While rodents frequently are seed predators for medium-sized and large seeds, secondary dispersal by scatter hording rodents can disperse seeds in a radius up to 100 m around a deposition site and burial can favor germination (Forget and Milleron 1991; Fragoso 1997; Brewer and Rejmanek 1999). To our knowledge no studies have looked at the post-dispersal fate of small and medium-sized seeds in tapir dung. Studies on primate dung have shown that secondary dispersal by dung beetles scatters seeds in a radius of up to 1.5 m around dung piles thereby reducing competition between seeds. Burial by dung beetles both increased germination rates and moves seeds out of reach of seed predators (Andresen and Levey 2004). Secondary dispersal by dung beetles decreases with increased seed size but increased with the amount of dung present (Andresen 1999; Andresen and Levey 2004). The large number of small seeds found in tapir dung together with the large amount of dung deposited and secondary dispersal by dung beetles could increase the number of seeds successfully dispersed by tapirs.

While tapirs might not be the single most important disperser for most species, they increase redundancy in seed dispersal services and increase the size and complexity of the seed shadow for many species. This could be important especially in areas where hunting has reduced the density of many of the large frugivores, with a large impact on the dispersal of large-seeded species (Peres and Palacios 2007).

CHAPTER V

EVALUATION OF A NEW GPS DEVICE FOR TRACKING LARGE MAMMALS IN DENSE TROPICAL FORESTS

Synopsis

Collars with an integrated global positioning system (GPS) allow researchers to collect a large number of accurate locations for wild animals. However, most GPS systems currently are unable to receive a signal under the dense canopy of tropical forest. This study tested a new system that promises highly improved performance due to a special signal processing algorithm. The system was tested at known locations to evaluate the performance and error distribution. In addition, it was tested on four free-ranging tapirs under typical field conditions.

The mean success rate for the stationary collars placed inside the forest was 87.3% (range 71.5-94.4%). The success rate for the tapir collars was 48.5% (range 38-58%). The mean location error for the stationary collars inside the forest was 28.9 m and the 95% error was 76.8 m. For collars placed in open areas, the mean error was 6.7 m and the 95% error was 14.1 m.

Several data screening options were evaluated and data screening based on the number of satellites used performed best. Data screening reduced the number of locations with large errors but at the same time also deleted a large number of good locations so that the adequate level of data screening has to be chosen carefully.

A data reduction of up to 40% had very little impact on the home range size and structure estimated with the fixed kernel method and the Brownian bridge movement model. Even at data reduction levels of 70% values for the volume index (VI) were all >0.8 indicating a high similarity of the full and the reduced utilization distribution (UD).

The results show the feasibility of GPS-based animal tracking in tropical forest using a new GPS system. This new technology will allow researchers to collect a large amount of data on the ecology, movement patterns and habitat use for many tropical forest species.

Introduction

Radio telemetry is a popular method for studying habitat use, movement patterns and survival of a wide range of animal species (Millspaugh and Marzluff 2001). Thousands of studies have used this technique in all parts of the world. However, there are only a handful of telemetry studies of large and medium-sized mammals from neotropical lowland forests. This can partly be explained by the difficulty of tracking animals with radio telemetry in dense lowland rainforests, often in remote areas with poor access due to limited transportation infrastructure. Many researchers have been forced to follow their collared animals through overflights by airplane (Rabinowitz and Nottingham 1986; Crawshaw 1995; Fragoso 1998), but aerial telemetry is dangerous and involves difficult logistics and high costs.

During recent years, GPS collars have become more popular in the studies of large herbivores and carnivores, especially in North America and Europe (e.g. Merrill *et al.* 1998; Bowman *et al.* 2000; Dyer *et al.* 2001; Beland and Follmann 2002; Adrados *et al.* 2003; Anderson and Lindzey 2003; Gau *et al.* 2004; Soisalo and Cavalcanti 2006). While these collars are relatively expensive they can collect a large amount of data and drastically reduce manual labor and airplane time. Unfortunately, conventional GPS collars perform poorly in tropical lowland forest. Rumiz and Venegas (2006) showed that while GPS collars worked in the dry forest of the Bolivian Chaco, they only obtained a successful fix in 1-3% of all intents in the lowland forest of the Madidi National Park, Bolivia. Collars tested for a forest elephant study in central Africa had a success rate of 9.8% in handheld trials in dense forest (Blake *et al.* 2001). The lack of any other published studies using GPS collars in tropical lowland forests suggests that few have used them successfully in this habitat type.

An ongoing study of the ecology of lowland tapirs (*Tapirus terrestris*) in the Peruvian Amazon required a system that would work in the dense forest and acquire data with a high temporal resolution. The present study evaluates a new system called TrackTag (NAVSYS Limited, West Lothian, UK). The TrackTag is a light-weight GPS that was designed to minimize battery consumption and weight. The TrackTag differs from

conventional GPS units used in most animal collars in that it does not perform any data processing at the time of signal acquisition. The TrackTag turns on for 32 milliseconds and during that time records raw GPS signal data (a snapshot). The data are stored in a non-volatile memory and later post-processed on a computer using advanced signal processing algorithms that are able to detect much lower signals than the algorithms currently used in most GPS units. The short on-time of 32 milliseconds (compared to up to 90 seconds for conventional GPS collars) drastically reduces battery consumption and allows the TrackTag to record in excess of 30,000 snapshots on as little as 200 mAh.

After initial field testing with a hand held unit in 2004, Advanced Telemetry Systems, Inc. (ATS) fabricated five collars for tapirs. The collars were based on ATS's large mammal GPS collar (model G2000) with the standard GPS unit replaced by a TrackTag circuit board. These collars had a VHF transmitter and a remote-controlled release mechanism and the function for up to 12 months while recording 30,000 snapshots. In 2006 NAVSYS developed a new fully integrated design (Tracktag electronics, GPS antenna and battery in a waterproof housing) that allowed the attachment of the complete assembly to a regular VHF collar. Both designs use the same GPS unit and antenna configuration.

Here I present initial results from the TrackTag GPS collars based on data obtained from stationary tests to evaluate location errors and from four collars deployed on tapirs. I evaluate different data screening options to remove large errors and test the influence of missing locations on home range estimation. I evaluate at the impact of data screening and biased data loss on home range estimation using the kernel and the Brownian bridge movement model methods.

Study Area

This study was carried out in the Los Amigos Conservation Concession, a 1400 km^2 protected area along the Madre de Dios and the Los Amigos Rivers in the Department of Madre de Dios (12°57' to 12°36' S and 70°02' to 70°09' W, elevations ranging from 250 to 320 m). Mean annual rainfall is 2500 to 3500 mm with a marked dry season from

June to September. Maximum precipitation falls during the months December through February and mean annual temperature is 24°C with a minimum of 10°C and a maximum of 38°C.

The vegetation is classified as a Southwest Amazon moist forest (Olson *et al.* 2001) with three major vegetation types; *terra firme* forest, floodplain forest and palm swamps dominated by the palm *Mauritia flexuosa*. *Terra firme* and floodplain forests are mature multi-layer tropical forest with trees reaching over 30 m in height. Canopy cover ranges from 70 to 100% and the average stem density is 800 stems/ha (diameter at breast height larger than 10 cm). The topography is generally flat, especially in floodplain forests. But terra firme forests are often dissected by multiple small to large streams that flow into the Madre de Dios and Los Amigos Rivers.

Materials and Methods

Stationary Tests

To evaluate the success rate and the error distribution of positions obtained by TrackTag GPS collars under dense vegetation cover, I set up an experiment where I ran the GPS unit at a fixed position over a period of one to two days. The units were programmed to take a snapshot every five minutes and were set horizontally at a height of 80 cm above the ground at least 2 m away from the closest tree. I chose 21 different sites; ten in *terra firme* forest, nine in floodplain forest and two at locations unobstructed by vegetation and with a clear view of the sky. All forest sites had a canopy larger than 85% and were representing the range of forest structure and tree density found in the area. The exact position of each site was marked with a Trimble GeoXT differential GPS and the data were post-processed against a base station less than 1 km away from the site. At least five minutes of data were recorded at each location with the GeoXT and the estimated horizontal position error was less than 2.5 m. Tests were done in October 2006 and between July and August 2007.

Tests on Animals

During 2005-2006, several lowland tapirs were captured and equipped with TrackTag GPS collars. The main goal of the study was to investigate the tapir's home range size, movement patterns, and habitat use, as well as their use of mineral licks. Tapirs were captured by darting them with a tranquilizer dart at a mineral lick. Some of the collars fell off prematurely. For this analysis I used data from four collars covering data periods of 23 to 102 days. Two of the collars were programmed to take a snapshot every 15 minutes, the other two every 10 minutes.

Data Analysis

The processed data from the GPS units include the following information: snapshot number, date, time, solution (3-D, 2-D or no fix), latitude, longitude, altitude, position dilution of precision (PDOP, an indicator for how satellite constellation affects precision), and satellite count (SVC, the number of satellites used to calculate the position). This information is being recorded regardless of whether a position was successfully calculated. To calculate errors from the true position I converted coordinates to UTM and then calculated the Euclidian distance to the reference location. I then calculated the maximum error as well as different error probabilities. A value of 100 m for the 95% error probability would mean that 95% of all positions had an error smaller or equal to 100 m. For both the stationary tests and the tapir collars I calculated the percentage of successful fixes as well as the distribution of PDOP and SVC values. Success rates were compared between forest types and stationary collars and collars on tapirs using a t-test.

Data Screening

Data screening aims to remove large location errors by filtering the data set based on an indicator variable such as PDOP or 2-D and 3-D fixes (D'Eon and Delparte 2005; Lewis *et al.* 2007). There are two possible variables that could be used to screen the data; PDOP and SVC. To find the most appropriate variable for data screening I looked at the correlation between the variable and the mean location error as well as the percentage of

locations with an error >100 m. I then tried a variety of different screening options based on minimum SVC, maximum PDOP and a combination of the two and compared error percentile, locations with large errors removed and total data reduction.

Impact of Data Loss on Home Range Estimation

Utilization distributions (UD; Vanwinkle 1975) have become a popular method for estimating home range size and use of space by animals (Marzluff *et al.* 2001; Millspaugh *et al.* 2006). UD are continuous surfaces showing the probability of use by an individual animal. Home ranges are then defined as the area where the summed probability of use reaches a certain level e.g. 95% or 50% (Powell 2000). The most widely used approach for estimating UD from point locations is the kernel method (Worton 1989). The Brownian bridge movement model (BBMM) is a new technique for estimating UD based on a mechanistic movement model (Horne *et al.* 2007a). The BBMM directly incorporates different time intervals between locations due to missing data as well as location errors into the model and potentially could be more robust to missing data.

All home range analyses were conducted in R using the "adehabitat" package (Calenge 2006). A bivariate normal kernel was used for the kernel estimator. I tried both the ad-hoc or reference method and the least square cross-validation (LSCV) method to estimate the smoothing factor h. The LSCV methods did not converge for most of the datasets, a problem common with data from GPS collars (Hemson *et al.* 2005). The ad-hoc method was highly variable for different sample sizes. Since the objective was to compare home range structure at different data levels and not to evaluate the performance of estimators for h, I decided to keep h fixed at h=150, which was approximately the average of the ad-hoc method for different datasets. For the BBMM I estimated the standard deviation of the location error from the stationary data (δ=40 m) and the Brownian motion variance parameter (σ_m^2) using the maximum likelihood method (Horne *et al.* 2007a). I removed the influence of parameter estimation by

averaging σ_m^2 for different data levels for each dataset. I used a grid size of 100 x 100 cells for all analyses.

To evaluate the impact of data loss caused by failed fixes on home range size and the shape of the UD I calculated UDs with both the kernel and BBMM methods from the tapir data using different data screening levels (SVC>3, SVC>4, SVC>5, SVC>6). Filtering on SVC is a biased data reduction, since more locations are removed from areas with poor satellite reception. I expect this to represent situations where data is lost due to environmental factors such as canopy or topography. I compared home range size at the 95% and 50% level and compared the similarity of the resulting UD using the volume of intersection (VI) at a 95% level. VI is an index with a value of one if two UD are identical and a value of zero if they are completely different (Fieberg and Kochanny 2005).

Results

Success Rates and Location Errors

The mean success rate for stationary collars under dense canopy was 87.3% (SD 6.15, range 71.5-94.4%). There was no significant difference between *terra firme* and floodplain sites (t = 0.9898, df = 11.002, p-value = 0.3435), thus the data from the two forest types were pooled for all following analyses. Success rates for the two opens sites were 99.4 and 100%. The mean success rate for the animal collars was 48.5% (SD 8.54%, range 38-58%) which was significantly lower than for the stationary collars (t = -8.6242, df = 3.683, p-value = 0.001). The mean number of satellites used to calculate a position was significantly lower for collars on animals than for stationary collars (animal: 5.12 SD 1.26, stationary: 5.82 SD 1.36, t = -38.5429, df = 17677.54, p-value < 0.0001), and it was lower for both groups compared to collars placed in the open (Figure 12a). Collars placed in the open had more locations in lower PDOP classes than collars placed inside the forest and collars put on tapirs had more locations in larger PDOP classes (Figure 12b). This shows the strong impact canopy cover has on satellite reception.

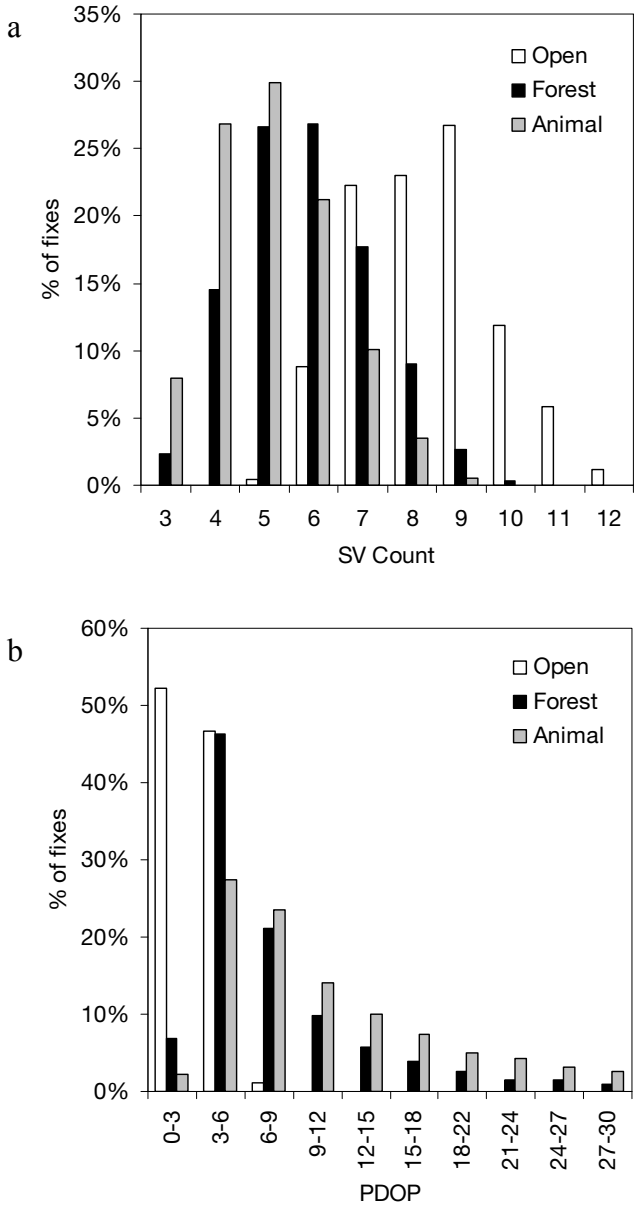

Figure 12: Distribution of the number of satellites (a) used to calculate a position and PDOP values (b) for GPS collars placed inside the forest, on free ranging tapirs and in an open clearing in the Peruvian Amazon.

The mean location error for forest sites was 28.9 m (SD 28.8 m) and was much larger than for open sites (6.7 m, SD 4.2 m). All locations in open sites had an error <30 m while forested sites had maximum errors of up to 400 m. However, even for forested sites only 2.8% of all locations had an error >100 m. Ninety-five percent of all locations had an error <76.8 m and 99% had an error <146.1 m (Table 14).

Table 14: Mean location errors for stationary TrackTag GPS collars placed at 19 forest sites and two open sites in the Peruvian Amazon.

	Location error (m)							
	Mean (SD)	50%*	95%*	99%*	100%*	>100 m	>200 m	Locations (N)
Forest	28.9 (28.8)	21.7	76.8	146.1	408.1	2.8%	0.4%	8707
Open	6.7 (4.2)	5.9	14.1	20.6	26.2	0.0%	0.0%	431

* Percentiles

Data Screening

Both PDOP and SVC are clearly correlated with the mean location error and with the number of locations with an error >100 m (Figure 13). The relationship is exponential for SVC and approximately linear for PDOP. Both variables should be useful for data screening and different filter levels for both of them were evaluated.

Data screening successfully reduced the number of locations with large errors (Table 15). However this reduction comes at a cost. The lowest filter level (SVC >3) removed about 4.8 locations with an error <100 m for every location with an error >100 m. This value increases linearly with the percentage of high-error locations that are removed and reaches 26.4 at the highest filter level (SVC >6). Therefore a trade-off exists between removing high-error locations and retaining low-error locations. In general the results show that data screening based on SVC or a combination of PDOP and SVC is more efficient than screening on PDOP. SVC >3 removes 18% of all high-error locations while only removing 2% of all low-error locations, while screening on PDOP<21 removes 16% of all high-error and 4% of all low-error locations. A combined filter on

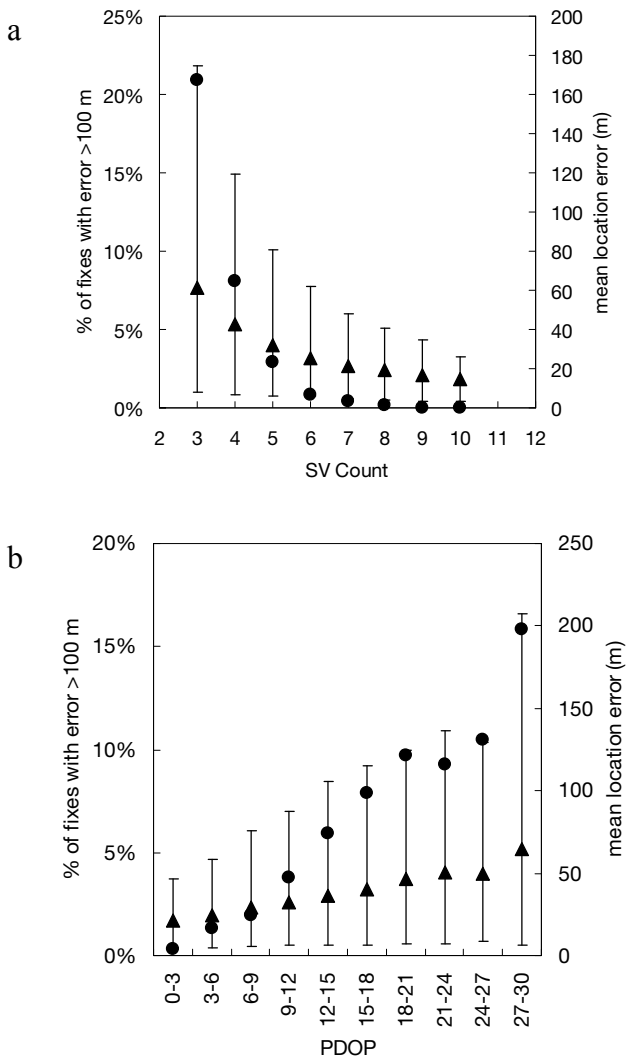

Figure 13: Percentage of locations with an error >100 m (dots) and mean location error (triangles) for different numbers of satellites (a) and PDOP values (b). Error bars indicate 5% and 95% percentiles for the location error. The data comes from GPS collars placed inside the forest in the Peruvian Amazon.

PDOP and SVC performs well when high data retention is the goal, removing between 28 and 49% of all high-error locations while only removing 5% and 11% of the low-error locations. Data reduction is larger for collars deployed on animals than for stationary collars due to the lager number of locations in lower SVC and higher PDOP classes which are the classes removed by data screening.

Table 15: Data reduction and error percentiles for different data screening options for GPS data from a forested site in the Peruvian Amazon.

	Data reduction (%)					Location error (m)			
Option	All[a]	>100[a]	>200[a]	Animal[b]	Cost[c]	50%	95%	99%	100%
All	0	0	0	0	0.00	21.7	76.8	146.1	408.1
SV>3	2	18	28	8	4.79	21.5	73.8	136.3	408.1
PDOP<21	4	16	28	10	8.79	21.3	73.3	139.7	408.1
PDOP<21, SV>3[d]	5	28	47	14	6.52	21.2	70.8	130.5	408.1
PDOP<21, SV>4[d]	11	49	58	27	8.29	20.7	66.3	122.9	402.5
SV>4	17	60	69	35	10.18	20.3	63.3	110.7	368.5
PDOP<11	19	55	58	36	12.36	20.3	64.3	120.7	402.5
PDOP<7	38	72	72	61	19.11	19.5	58.3	107.9	368.5
SV>5	44	88	97	65	17.87	18.8	53.1	87.9	316.8
SV>6	70	97	100	86	26.39	17.5	44.9	69.1	132.8

[a] data from stationary collars, [b] data from collars deployed on four tapirs, [c] number of locations with an error <100 m filtered for each location with an error >100 m, d SVC was only filtered for PDOP>10.

Impact of Data Loss on Home Range Estimation

A data reduction of up to 40% had very little impact on both the shape of the UD and the size of the home range estimation for both the kernel method and the BBMM (Table 16 and Table 17). UD were very similar with all VI values >0.8 up to 70% data reduction, even for a data reduction of 80%-90% the UD were still highly correlated with most VI values >0.75 and some as high as 0.904. At approximately 60% data reduction, home range estimates began to vary with increases and decreases of up to 60% in size. At a reduction level of 80%-90% home range sizes can be more than twice or less than half the size of the home range for the full dataset. VI values in all cases were higher for the kernel estimator than for the BBMM. For home range estimation neither of the two methods performed had a clear advantage.

Table 16: Comparison of the 50% and 95% home range size using the kernel (KHR) and Brownian bridge movement model (BBHR) estimators under different data reduction schemes. Data reduction was carried out by filtering on the minimum number of satellites (SV) used to obtain a location.

	Tapir 1 (N=1683)				Tapir 2 (N=6867)			
SV	50% KHR	95% KHR	50% BBHR	95% BBHR	50% KHR	95% KHR	50% BBHR	95% BBHR
All	100	337	45	214	68	403	30	279
>3	99	337	45	215	69	405	32	277
>4	99	335	46	212	69	406	37	288
>5	100	334	52	223	66	400	50	298
>6	98	333	64	244	61	373	72	351

	Tapir 3 (N=1231)				Tapir 4 (N=3187)			
SV	50% KHR	95% KHR	50% BBHR	95% BBHR	50% KHR	95% KHR	50% BBHR	95% BBHR
All	24	218	16	148	59	352	39	200
>3	22	202	15	136	60	350	39	198
>4	18	166	15	154	58	339	41	209
>5	16	128	14	142	54	337	40	258
>6	14	87	13	113	50	319	55	413

Values show the home range size for four tapirs in hectares. The number of locations for the full dataset is given for each individual. The percentage of data reduction is given in Table 17. The data were collected with GPS collars in the Peruvian Amazon.

Table 17: Comparison of the UD from kernel (K UD) and Brownian bridge movement model (BB UD) estimators under different data reduction (DR) schemes.

	Tapir 1 (N=1683)			Tapir 2 (N=6867)			Tapir 3 (N=1231)			Tapir 4 (N=3187)		
SV	BB UD	K UD	DR	BB UD	K UD	DR	BB UD	K UD	DR	BB UD	K UD	DR
>3	0.977	0.993	5%	0.969	0.981	8%	0.963	0.976	6%	0.968	0.989	9%
>4	0.946	0.977	23%	0.901	0.938	35%	0.891	0.902	33%	0.93	0.95	40%
>5	0.886	0.952	56%	0.801	0.878	64%	0.765	0.848	66%	0.846	0.895	70%
>6	0.797	0.904	84%	0.673	0.829	84%	0.622	0.795	90%	0.705	0.835	88%

Data reduction was carried out by filtering on the minimum number of satellites (SV) used to obtain a location. The values show the volume of intersection (VI) comparing the UD from the reduced dataset to the UD from the full dataset; a value of 1 means that the two UD are identical and 0 means that they are completely different. The number of locations for the full dataset is given for each individual. The data was collected with GPS collars in the Peruvian Amazon.

Discussion

The TrackTag GPS collars performed well in all of the tests. Success rates of 70% to 95% for stationary collars under canopy and 38% to 58% for collars deployed on animals are comparable to results obtained by conventional GPS collars under the canopy of temperate forests (Rempel *et al.* 1995; Frair *et al.* 2004; Lewis *et al.* 2007; Sager-Fradkin *et al.* 2007). The fix rates of the collars deployed on tapirs were markedly lower than the fix rates of stationary collars. But this is commonly found with GPS collars (Cargnelutti *et al.* 2007; Lewis *et al.* 2007; Sager-Fradkin *et al.* 2007). There are several possible explanations why collars on animals would have a lower success rate. Due to the tapir's crest, the orientation of the collar antenna is often not completely horizontal but can be up to 60 degrees inclined. This inclination can have an negative impact on success rate (D'Eon and Delparte 2005) and this effect will be amplified by the low signal strength and few available satellites under dense forest canopy. Both the size of the animal (Graves and Waller 2006) and its behavior, such as bedding (Moen *et al.* 1996; Sager-Fradkin *et al.* 2007), can also reduce success rate. While a success rate of about 50% seems relatively low, this is partly compensated by the ability of TrackTags to record a large number of locations. With a typical acquisition interval of 15 minutes, for a 12 months deployment, the average number of successful locations per day is between 40 and 50. This is a huge amount of data that allow researchers to study detailed daily movement patterns (Figure 14). However, the potential bias for habitat studies and home range estimators introduced by missing data has to be considered in the analysis, as discussed bellow.

Location errors were significantly larger under dense canopy than in open areas but were within the range of errors reported for other GPS collars in temperate forests (Cargnelutti *et al.* 2007; Lewis *et al.* 2007; Sager-Fradkin *et al.* 2007). There are multiple reasons for an increase in error inside the forest. Satellite availability is reduced due to blocked and weak signals. Other important sources of error are multipath (the signal is being reflected by trees or topography causing the signal to travel farther) and a low signal-to-noise ratio. The algorithms used to process the TrackTag data are optimized for

detecting weak signals and therefore can increase the number of satellites available compared to conventional GPS receivers. However, they can not remove errors resulting from multipath.

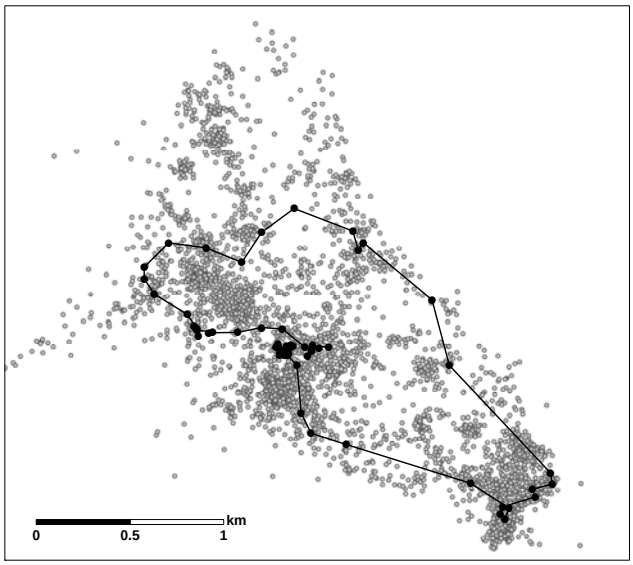

Figure 14: Location data from a tapir collected with a TrackTag GPS collar in the Peruvian Amazon. Grey dots show all locations (N=5800) collected during 103 days. The black line shows an example movement path for the animal during a 24 hour period. The clumps of locations at the beginning and the end of the path show resting sites.

Most previous studies have focused on PDOP or 2-D or 3-D fixes for data screening (Moen *et al.* 1996; Dussault *et al.* 2001; D'Eon and Delparte 2005; Lewis *et al.* 2007). For the datasets presented here SVC was a better predictor of high location errors, and screening options using SVC or a combination of SVC and PDOP performed better than the ones based on PDOP only. While SVC and PODP are good predictors for the mean location error, they perform poorly for predicting individual location errors (Rempel *et al.* 1995; D'Eon and Delparte 2005; Graves and Waller 2006; Lewis *et al.* 2007). This is mostly due to the large standard deviation of the error distribution which for the data was almost equal to the mean for all SV and PDOP classes (coefficient of variation 0.7-1). As a consequence, data screening based on these two variables is not very selective and

many acceptable locations are excluded together with those locations that exhibit large errors.

Moderate data screening (PDOP<21, SV>4) only slightly improved the 50% and 95% error probabilities but it was successful in the removal of up to 50% of all locations with an error >100 m, while only removing 11% to 27% of good positions. Further reduction of locations with large errors was associated with increased costs and might not be justified for most applications. While it was possible to get the 99% error probability below 100 m, this was associated with a 70% data reduction for stationary collars and 86% data reduction for collars placed on tapirs. Screening with the PDOP<21 and SV>3 or PDOP<21 and SV>4 should be most appropriate for these data for most applications. A 95% error of <100 m seems to be a safe assumption for the analysis of TrackTag data from tropical forests.

While data screening reduces the problem of large location errors in the data, it increases another important problem for data analysis, that of missing data (D'Eon and Delparte 2005). Data screening aimed at removing large errors will often remove points associated with denser habitat types or with activities such as resting, where satellite reception was impaired. This can amplify bias toward more open habitats in a dataset. If one considers that less than 5% of all locations have an error >100 m, one has to weigh carefully if the increase in lost data might not be a more serious problem than a few points with a large error. Frair et al. (2004) showed how an increase of data loss from 10% to 30% drastically increased the type II error rate for some habitat types in an analysis using resource selection functions. They proposed a bias correction method to reduce bias due to data loss. Horne et al. (2007b) proposed an error correction for kernel home range estimator. However, their method requires the estimation of fix success probabilities for different discrete habitat types, something often impossible in tropical lowland forests that are very heterogeneous on a small scale but relatively homogeneous on a large scale.

Most studies that evaluated the effect of sample size on kernel home range estimators used random sub-samples (Seaman *et al.* 1999; Girard *et al.* 2002). This is an

appropriate design to estimate minimum sampling effort, but it does not give much information on the effect of biased data loss due to environmental effects. The results from this study show that even with a biased data reduction of over 50% the general structure of the UD was only slightly affected. Core areas were still identified correctly in all of the test datasets. UDs for different reduction levels estimated with the kernel estimator were usually more similar than the ones from the BBMM but this can partly be related to the amount of smoothing chosen for the two estimators. Figure 15 shows that the kernel estimator produced somewhat smoother contours than the BBMM with the smoothing factors chosen for the analysis. Also, the way the BBMM estimates the UD differs greatly from the method used by the kernel estimator. While the kernel estimator only uses the remaining locations, the BBMM tries to interpolate missing locations using a "bridge" between two existing locations. This can introduce additional differences between the full and the reduced UD.

The 50% and 95% home range areas were stable for low and medium data reduction but increased bias started showing above 50% data reduction for some datasets. Bias can be positive or negative and largely depends on the data. Figure 15 shows two examples. In the first case (Figure 15 a and b), the home range area for both the 50% and the 95% home is very stable and hardly changes even with a 84% data reduction. This indicates that the forest in that area is fairly homogeneous (which has been confirmed by observations in the field), and that there is very little bias in the reduced data. In the second example (Figure 15 c and d), most locations in the upper right part of the home range were removed, resulting in a drastic decrease of home range size. The reduction of the data seems to be strongly biased and this is reflected in the results at high reduction rates. The strong bias can be explained by the forest structure in that area; the area with a high number of locations is a palm swamp which is much more open than the surrounding forest. The data shows that the general structure of a home range is maintained at levels of up to 50% data loss for datasets with a strong bias and up to 85% of data loss of relatively unbiased datasets.

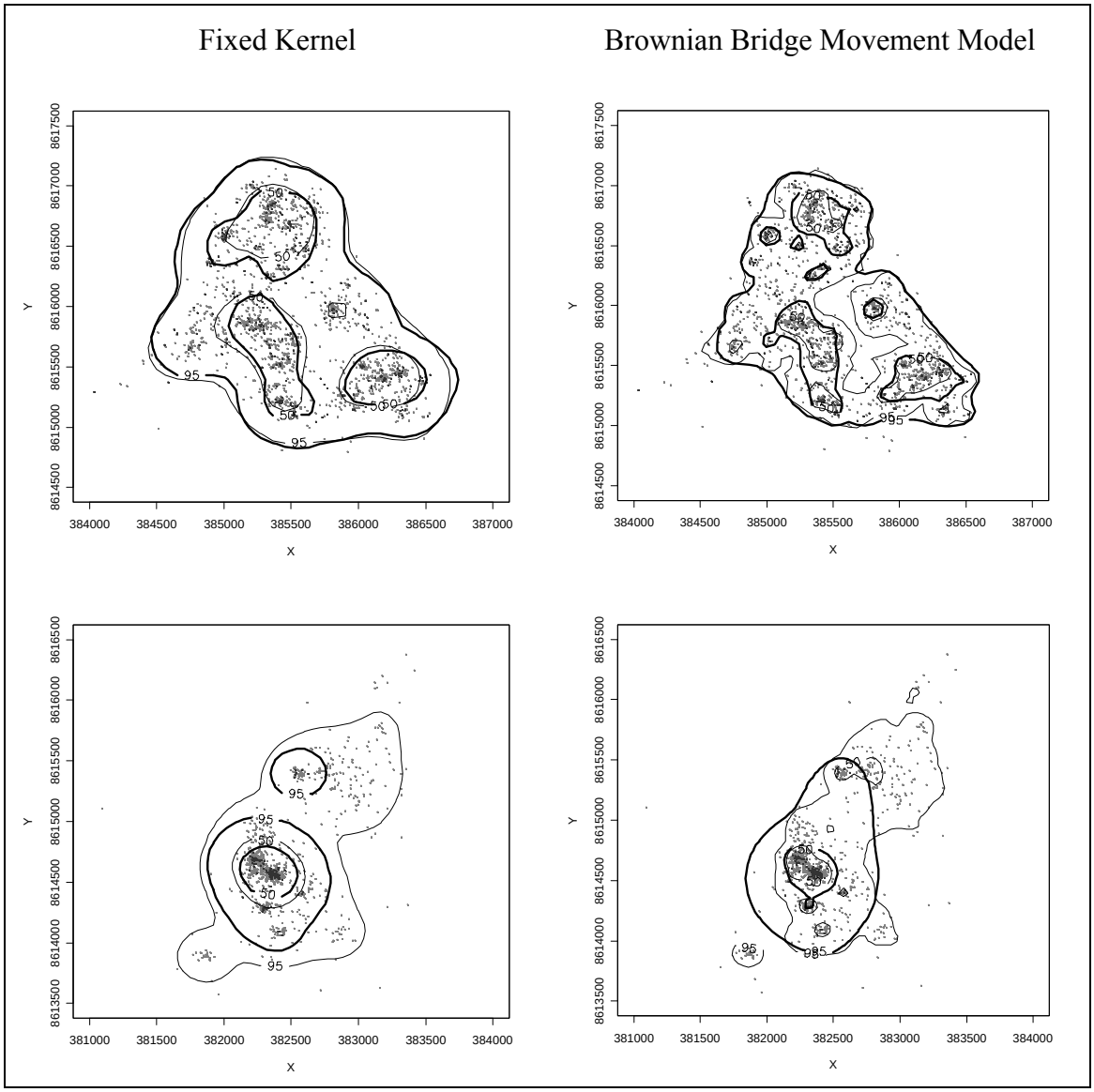

Figure 15: A comparison of home range estimates using a kernel estimator and a Brownian bridge movement model. Lines show different percentiles. Thin lines are estimates using all locations, thick lines are estimates using only locations that used 6 or more satellites (SVC>6) witch resulted in a data reduction of 84% for the first dataset and 90% for the second one. Data was collected with GPS collars from two tapirs in the Peruvian Amazon.

Home range size varies strongly at high data reduction levels for biased datasets but was very stable for unbiased datasets. The VI for the full and a strongly reduced dataset might be useful as an index for the expected bias present in the data but the exact relationship would have to be evaluated with simulation studies. Based on results by Moser and Garton (2007), location error should have a small impact on the UD and home range estimation for our data, since the error ratios ($ER=CEP_{50\%}^2*Pi/$home range size) were all between 0.001 and 0.01 and sample size was usually in the order of several thousand locations. The increase in precision gained from data screening will therefore be outweighed by the introduction of extra bias in the data.

The results of this study show that TrackTag GPS collars perform well under the dense canopy of an Amazonian forest. Success rates and errors are comparable to data from other GPS collars in temperate forests. With the ability to record a large number of locations, the TrackTag collars can collect detailed data on movement patterns and the home range structure of study animals. These collars have great potential for studying large and medium-sized mammals in tropical forest and therefore will be able to fill many gaps in our knowledge of these animals.

CHAPTER VI
MOVEMENT PATTERNS AND HOME RANGE SIZES OF LOWLAND TAPIRS IN THE PERUVIAN AMAZON

Synopsis

Between 2005 and 2006 six lowland tapirs, four females and two males, were captured and equipped with GPS collars. The collars recorded between seven and 182 days of data resulting in 78 to 6185 locations. Mean fix success rate for all collars was 40%. Tapirs were mostly nocturnal, spending most of the day resting. Kernel home range sizes at the 95% level were between 102 and 386 ha. Home ranges encompassed multiple centers of activity which differed between day and night, showing that there are distinct resting places and feeding areas frequently visited by tapirs. The data from two different years for one individual showed that tapirs can have stable home ranges with clearly defined boundaries. Habitat use varied with the availability of habitat types within the animals' home range. Three individuals spend over 90% of their time in *terra firme* forest while the other two spent between 30 and 50% in *terra firme*, 30 to 40% in a *Mauritia flexuosa* palm swamp and the remainder in floodplain forests. One tapir infrequently visited a palm swamp outside its main range and another individual expanded its range into a nearby palm swamp showing active selection of this habitat.

Tapirs walked up to 10 km from their core area to visit mineral licks. The interval between visits varied greatly between one day and as much as 36 days. Most individuals visited between two and three different licks, all within the same general area; trails were well established between their home ranges and the licks. Mineral licks are an important resource for tapirs and require special attention in conservation planning and management for this species.

Introduction

Lowland tapirs occur throughout South America from Colombia and Venezuela to northern Argentina, at elevations up to 2000 masl (Taber *et al.* 2006). They inhabit many ecoregions from Amazonian lowland forests to savanna wetlands in the Pantanal and the dry forests of the Chaco and Cerrado, with the largest populations currently existing in the Amazon (Brooks *et al.* 1997; Taber *et al.* 2006). Tapirs are threatened throughout their range by hunting and habitat destruction. While the diet of lowland tapirs has been studied by several researchers (Bodmer 1991a; Rodrigues *et al.* 1993; Salas and Fuller 1996; Fragoso and Huffman 2000; Galetti *et al.* 2001), only two studies thus far have successfully collected data on home range size and movement patterns; one in the Bolivian Chaco (Ayala 2003) and the other in the Atlantic forest of Brazil (P. Medici pers. comm.). Information on home range size, movement patterns and habitat use is important for evaluating the suitability of protected areas for maintaining viable tapir populations, for estimating population densities, and for developing management plans. Most previous studies evaluated habitat use by track counts or other indirect signs (Bodmer 1991a; Salas 1996; Herrera *et al.* 1999) that can lead to biased results due to differences in the substrate between forest types (Salas 1996).

Tapirs use mineral licks in many regions and they are among the species that most frequently use licks in the Amazon (Ayala 2003; Montenegro 2004; Pfeifer Coelho 2006; Chapter III). Montenegro (2004) hypothesized that tapirs use licks to supplement minerals lacking in their diet, mostly Na, P, Cu and Zn, which indicates that mineral licks are an essential resource for tapirs in the western Amazon. While Herrera et al. (1999) collected some data indicating that tapirs will walk long distances to visit licks, and Montenegro (1998) collected the first data on the frequency of visits by individual tapirs, very little is known about the patterns of lick use by tapirs, the distribution of their home ranges in relation to lick locations, and the importance of licks for tapir populations in a region.

Previous studies experienced great difficulties tracking tapirs in dense tropical forests (Herrera *et al.* 1999). This study relied on a new type of GPS collar that uses sophisticated signal processing algorithms to track weak satellite signals under dense forest canopy (Chapter V). GPS collars have the great advantage that they can collect data at short time intervals, both day and night, and therefore show continuous movement patterns. The objectives of this study were to: 1) to collect detailed information on tapir home range sizes as well as the internal use of that range, 2) collect data on the distance walked by tapirs to visit mineral licks, and 3) document the frequency of lick visits by tapirs.

Study Area

This study was carried out in the Los Amigos Conservation Concession in Madre de Dios, Peru (12°30' to 12°36' S and 70°02' to 70°09' W, elevation 250 to 320 m). The concession is a privately managed protected area established in 2001 protecting the watershed of the Los Amigos River, a tributary to the Madre de Dios River. It is surrounded by active logging concessions where selective logging is taking place. The vegetation is classified as lowland Amazonian moist forest and four major habitat types can be distinguished; *terra firme* forest, floodplain forest and palm swamps dominated by *Mauritia flexuosa*. Patches of bamboo and multi-stage successional forests occur to a lesser extent.

The climate is tropical with mean annual rainfall between 2500 and 3500 mm, with a dry season from May to September and a rainy season during the months of November through February. Mean annual temperature is 24°C with a range from 10 to 38°C.

Materials and Methods

Captures

Tapirs use mineral licks with a high frequency in our study area (Chapter III). Taking advantage of this behavior, a platform with a blind was erected about three meters above the ground at one of the licks. The tapirs were shot with a tranquilizer dart fired from a

CO_2-powered rifle (Pneu-Dart Inc.) when they entered the lick to eat clay. Darts were loaded with a mixture of the narcotic butorphanol (45 - 55 mg/animal) and the alpha-2 xylazine (120-150 mg/animal) for an estimated weight of 200-250 kg of an adult tapir (Hernandez-Divers and Foerster 2001). If needed the anesthesia was supplemented with an intramuscular injection of ketamine (250 mg). The anesthesia was reversed with naltrexone (135 mg) and yohimbine (70 mg) given intramuscularly. All animals were fitted with a GPS collar and an ear tag for later identification.

Collars

For this study a new GPS system based on the TrackTag GPS (NAVSYS Limited, West Lothian, UK) was used. The TrackTag GPS has a much better performance under dense canopy than conventional GPS units and can record up to 30000 locations with a 95% error <100 m inside the forest (Chapter V). The collars used in 2005 were made by Advanced Telemetry systems, Inc. based on their large mammal GPS collar (model G2000) with the standard GPS unit replaced by a TrackTag. In 2006 NAVSYS developed a new design that allowed us to attach the GPS unit to a regular VHF collar (MOD 500, Telonics Inc., Mesa, AZ). Both designs used the same GPS and antenna configuration and had a VHF transmitter and a drop-off mechanism. Collars were programmed to record a position every 10 to 15 minutes and were deployed for periods of six to 12 months. Data were processed by NAVSY using their proprietary algorithm.

Data Analysis

Data screening is a process of filtering GPS collar data with the goal to remove locations with possible large position errors (D'Eon and Delparte 2005). Data from all collars was screened by filtering out positions with a PDOP (Position Dilution of Precision) larger then 20 and positions with a PDOP between 10 and 20 that used less than four satellites to calculate the position (Chapter V).

A bivariate normal kernel was used to estimate utilization distributions (UD) and home ranges for all tapirs (Worton 1989). The kernel method has the advantages over simple methods such as the minimum convex polygon (MCP) in that it not only outlines the

outer home range boundary but also describes the internal structure of a home range and allows for multiple centers of activity (Powell 2000; Kernohan *et al.* 2001). Since the least square cross-validation (LSCV) failed to estimate the kernel smoothing parameter h and the reference methods suggested relatively large values, h was set equal to 100 meters for all datasets. A distance of 100 meters is about equal to the 95% GPS error and gave good results for all datasets. A 95% volume level was used to define the full home range size and 25% and 50% levels to delineate core areas within the home range. MCP home ranges at a 95% level are reported for comparative purposes. Since MCPs are very sensitive to outlier points, all long-distance movements (e.g. visits to licks) were removed from the data to estimate the MCP of the main areas.

To investigate which areas of the home range were used for resting and for foraging, the data were divided into two sets: 1) one set contained all the locations taken during the day (9:00-16:00) when tapirs were mostly resting (see results below), and 2) the other contained nightly locations (18:00-4:00) associated with foraging. Locations in the early morning and late afternoon were excluded since that was the time the animals would usually move between feeding areas and resting areas. UD were calculated for both sets and the overlap was compared using the volume intersection index (VI) at the 50% and 95% level (Fieberg and Kochanny 2005). VI is an index that has a value of one if two UD are identical and a value of zero if they are completely different. This index compares both the general overlap of two home ranges, as well as their internal structure. All analyses were carried out in R using the "adehabitat" package (Calenge 2006).

To evaluate habitat use, a habitat map was manually digitized from a Landsat ETM image from 2004 in ArcGIS (Environmental Systems Research Institute, Inc.). Three major habitat types were distinguished: *terra firme* forest, floodplain forest and palm swamps. To compare habitat use, the time the animal spent in each habitat type was calculated from the GPS locations and the corresponding time stamps. This had the advantage over simply counting the number of locations in each habitat type because it removed bias introduced by different GPS success rates in different habitats.

Since the GPS collars used did not include an activity sensor, activity patterns had to be inferred from the movement data. This was done by identifying groups of locations where the animal remained within a circle with a 100 m radius (corresponding to a possible 100 m GPS error) for a period of at least two hours. All locations within such a group were classified as inactive and all other locations were defined as active.

Distances traveled to mineral licks and visitation rates were measured by visually examining the data in ArcGIS.

Results

Study Animals and Collar Performance

Between July and December 2005 seven individual tapirs were captured; six females and one male. One of the females captured in 2005 was re-captured in December 2006 and fit with a second collar. In April 2007 a male was captured. All animals were adults and all were captured at the same mineral lick.

At the beginning there were several problems with the collar attachment. The second tapir collared (TTF 3) lost its collar after only 7 days (Table 18). Two collars fell off after 26 and 22 days (TTF 5 and TTF 6, respectively). The collar from TTM 7 stayed on for a whole year but the GPS stopped recording data after 24 days. The collar from TTF 1 (A) also stayed on for a whole year but success rated declined and the collar stopped taking data after six months. The second collar put on TTF 1 (B) was programmed to record data for six months but batteries for the GPS failed after 102 days. The collar from TTP 10 had battery problems after 58 days. Collars from two animals were lost because of a failure of the VHF transmitter.

Table 18: Information on the data collected by GPS collars from six different tapirs in the Peruvian Amazon.

Animal	Sex	Start Date	End Date	Days	Locations	Success rate (%)[a]	Interval (min)[b]
TTF 1 A	female	11.07.2005	09.01.2006	182	6185	35.2	15
TTF 1 B	female	08.12.2006	20.03.2007	102	5884	39.7	10
TTF 3	female	06.08.2005	13.08.2005	7	78	10.2	15
TTF 5	female	29.08.2005	24.09.2005	26	1219	47.2	15
TTF 6	female	29.09.2005	21.10.2005	22	908	42.2	15
TTM 7	male	17.10.2005	10.11.2005	24	1098	45.9	15
TTM 10	male	03.04.2007	30.05.2007	57	2857	32.7	10

Start date indicates the capture data the end date indicates the data the collar stopped collecting data. [a] success rate after data screening, [b] data acquisition interval.

Mean fix success rates after data screening was 40% (range 33-47%, not including TTF 3). The reason the collar from TTF 3 had a much lower success rate was that the data was processed with an older algorithm that was later improved. There are only seven days of data available from that collar, so that it was excluded from most of the analyses.

Home Ranges and Habitat Use

Tapirs caught at a mineral lick had their home ranges in a wide area around the lick (Figure 16). Two animals walked about 10 km to visit the lick, two about 3 km and two had their home range less then 1 km from the lick. Four tapirs (TTF 1, TTF 3, TTF5 and TTM 10) had their main range entirely in *terra firme* forest. TTF 6 and TTM 7 occupied an area that included a large patch of palm swamp and surrounding floodplain forest, but also a good portion of *terra firme* forest (Figure 17).

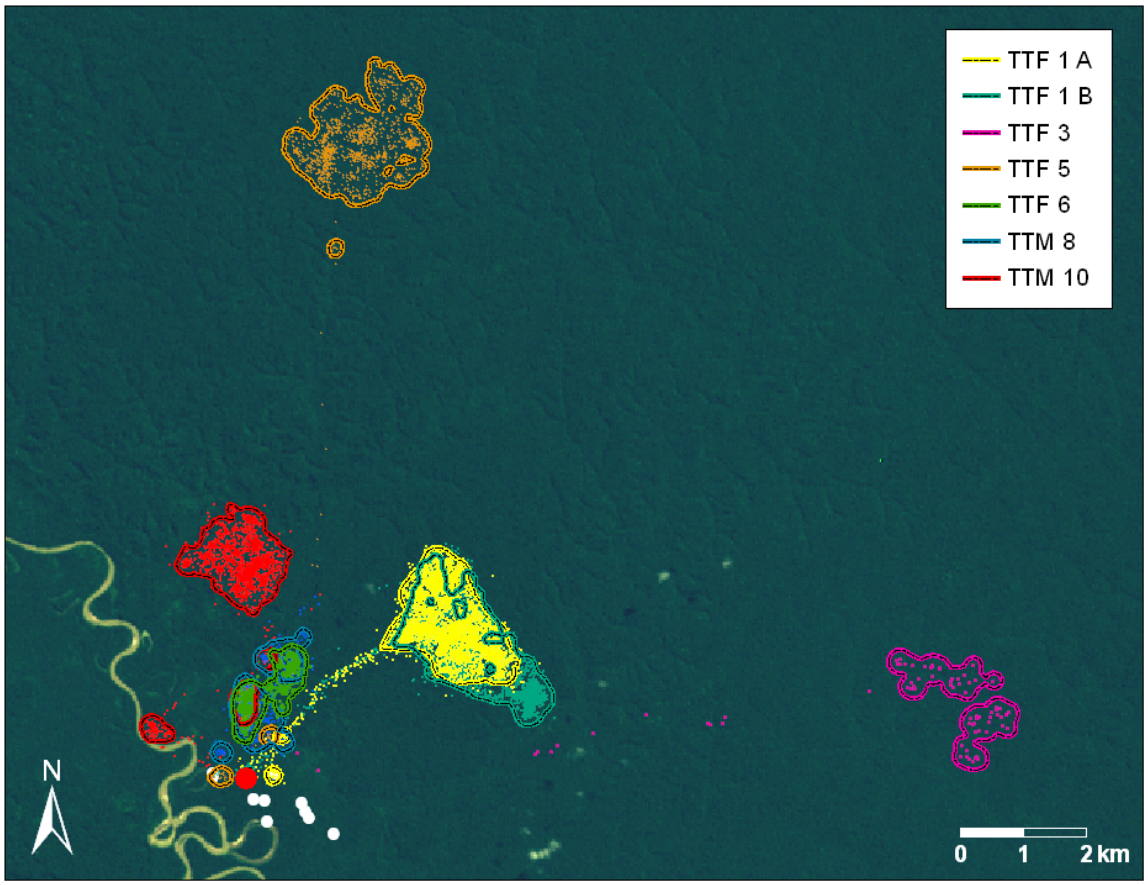

Figure 16: GPS collar locations and 95% kernel home ranges for six tapirs in the Peruvian Amazon. The red dot in the lower left part indicates the mineral lick where all animals were captured. The white dots show other mineral licks in the area.

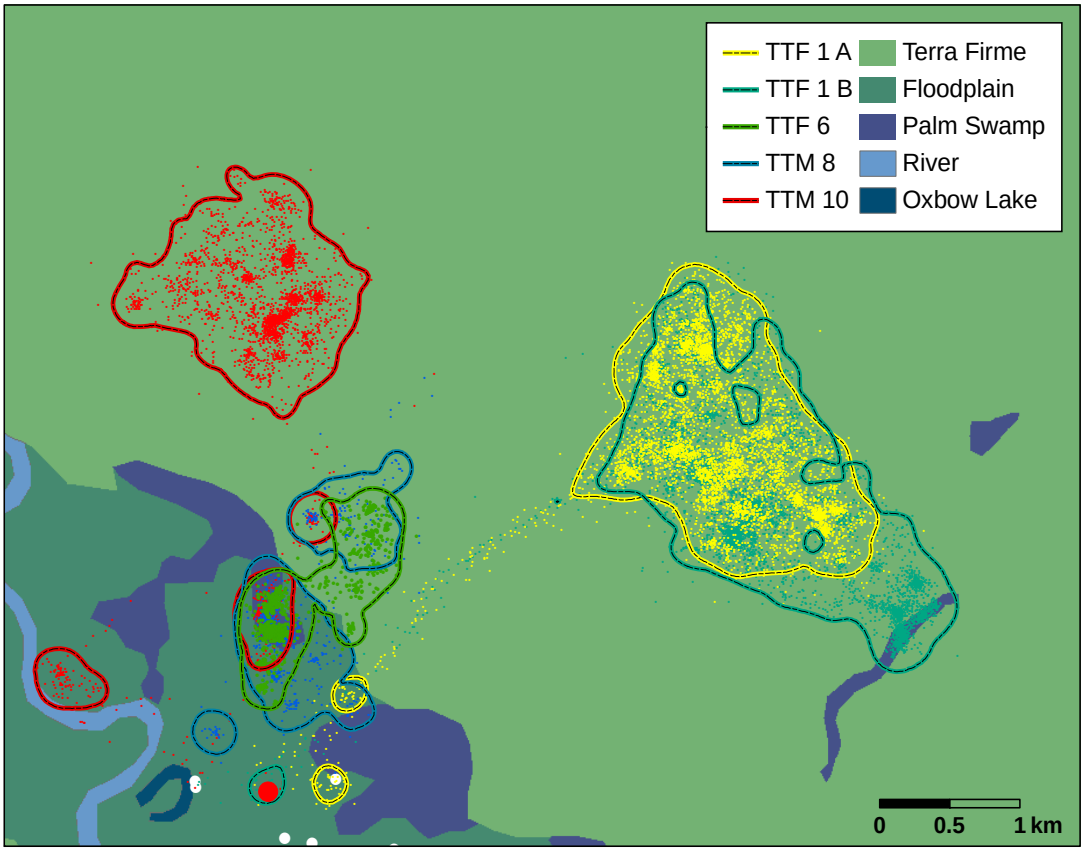

Figure 17: GPS collar locations and 95% kernel home ranges for four tapirs in the Peruvian Amazon. The red dot in the lower left part indicates the mineral lick where all animals were captured. The white dots show other mineral licks in the area.

Table 19: Home range sizes in hectares for five different tapirs from the Peruvian Amazon.

	Kernel HR			MPC[a]	Kernel HR day		Kernel HR night	
Animal	25%	50%	95%	95%	50%	95%	50%	95%
TTF 1 A	33	82	307	263	10	140	64	395
TTF 1 B	15	48	345	353	44	175	106	384
TTF 5	32	88	386	300	53	251	91	389
TTF 6	7	20	106	95	13	101	22	100
TTM 7	5	14	154	176	9	73	54	201
TTM 10	17	48	267	155	35	177	53	297

Data was collected with GPS collars. Kernel home ranges were estimated using a bivariate kernel with a smoothing factor h=100. Day locations include locations taken between 9:00 and 17:00, night locations were taken between 18:00 and 4:00. MPC: Minimum Convex Polygon home range.

Home range size varied widely between animals. The 95% kernel home range areas were between 102 and 386 ha, and the 50 percent core areas ranged from 17 to 88 ha. (Table 19). Estimates from the kernel and the MCP method were usually very similar.

The mean distance moved during a 24-hour activity period from 12 noon to 12 noon the next day was 5.2 km (range 3.6-6.7 km,) with maximum distance of up to 13 km for individual animals (Table 20). The distance moved was positively related to home range size ($F=46.8$, $df=423$, $R^2=0.1$, $p<0.001$).

Table 20: Daily distance moved in meters for five tapirs based on GPS collar data.

	Distance (km)			
Animal	Average	Min	Max	SD
TTF 1 A	4.7	0.9	13.2	2.3
TTF 1 B	6.7	3.2	12.7	1.8
TTF 5	6.4	2.6	12.8	2.1
TTF 6	3.6	2.2	4.6	0.7
TTM 7	4.9	2.3	7.2	1.1
TTM 10	5.4	1.5	11.5	2.1

Since tapirs are nocturnal, the time from noon until noon the next day was defined as a day.

The two home ranges of TTF 3 and TTM 7 overlap by 100 percent and both individuals spent a large amount of time in a palm swamp in the southwestern part of their ranges. TTF 1 expanded its home range by approximately 40 ha from 2005 to 2006 and started using a palm swamp located in a *terra firme* creek. TTM 10 regularly used areas outside its main range. One of these areas was a palm swamp inside the home range of TTF 3 and TTM 8, and another one was an area of floodplain forest next to the river.

Tapirs typically used different areas for foraging at night than they used for resting during the day (Figure 18). This difference is especially clear at the 50% level where, for several individuals, there was very little overlap and a low similarity between daytime and nighttime home ranges (Figure 18). TTF 1 (A and B), TTF 5 and TTM 10 have a relatively complex home range structures, with two to three different centers of activity

both at night and during the day. All tapirs had defined resting sites they used repeatedly over a longer period of time. The home ranges for TTF 3 and TTM 7 are simpler, with only a single center of activity.

Table 21: Similarity between tapir's kernel home ranges based on daytime and nighttime locations from GPS collars.

Animal	VI[a] 50%	VI 95%
TTF 1 A	0.105	0.497
TTF 1 B	0.085	0.280
TTF 5	0.236	0.439
TTF 6	0.489	0.629
TTM 7	0.388	0.520
TTM 10	0.478	0.604

[a] Volume Intersection Index

A difference between day and night can also be seen in the habitat use of several individuals (Table 22). TTF 6 spends less time in the palm swamp and more time in the surrounding floodplain forest during the night. TTM 7 also spends less time in the palm swam and increases use of *terra firme* and floodplain forest during the night. TTF 1 and TTF 10 on the other hand use palm swamps exclusively during the night. TTF 1, TTF 5 and TTM 10 spend over 90% of their time in *terra firme* forests while TTF 6 and TTM 7 use all three habitat types.

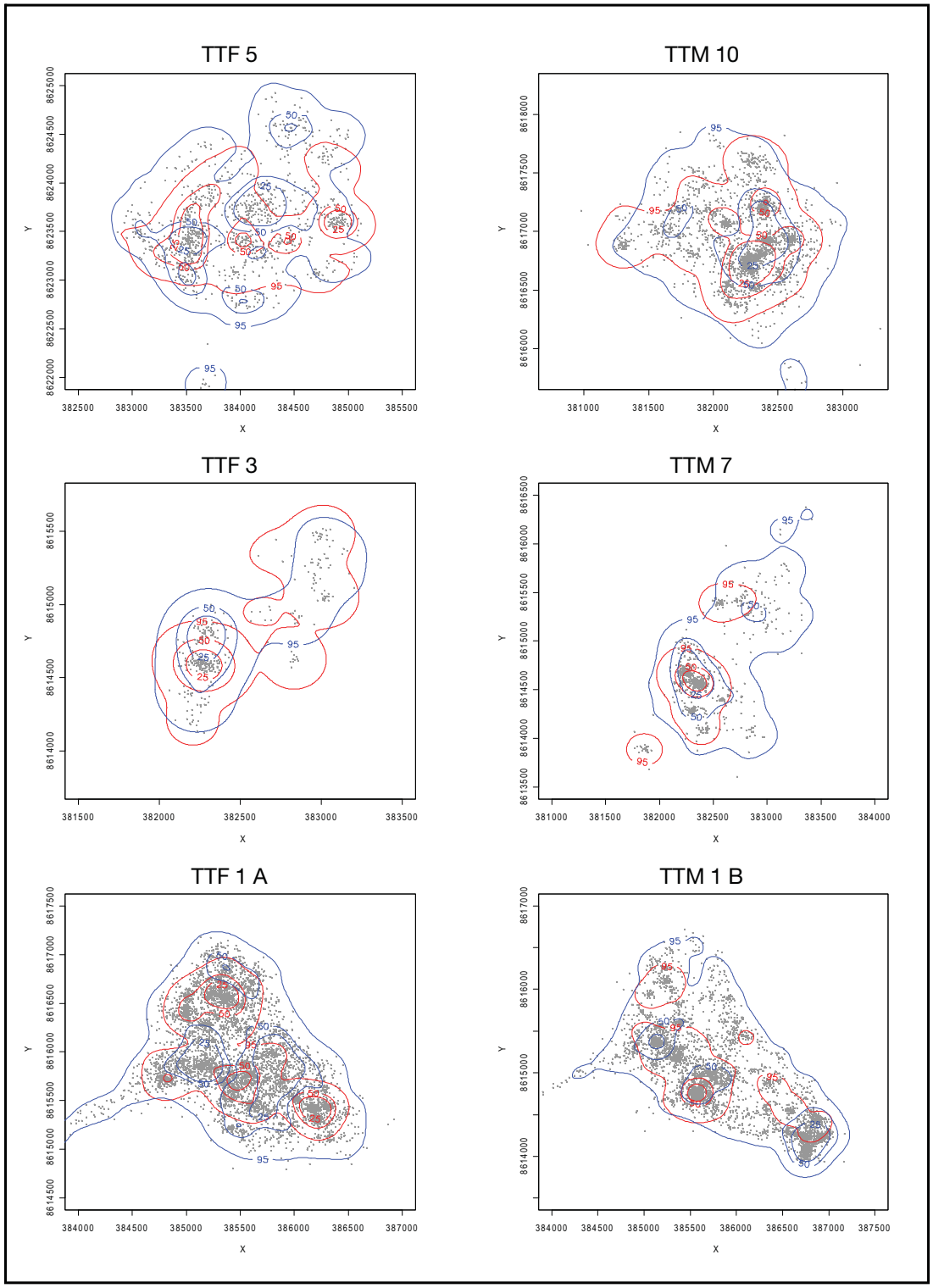

Figure 18: Kernel home range estimates for five different tapirs tracked with GPS collars in the Peruvian Amazon. Red lines are based on daytime locations (9:00 -17:00), blue lines on nighttime locations (18:00-4:00).

Table 22: Habitat use by five different tapirs in the Peruvian Amazon.

		Use			Available		
Animal		PS	FP	TF	PS	FP	TF
TTF 1 A	Day	0.0	0.0	100.0			
	Night	1.0	2.8	96.2			
	Both	0.5	1.4	98.1	2.5	8.7	88.8
TTF 1 B	Day	0.2	0.0	99.8			
	Night	12.1	2.6	85.3			
	Both	5.6	1.2	93.2	2.0	5.7	92.4
TTF 5	Day	0.0	3.7	96.3			
	Night	0.0	0.7	99.3			
	Both	0.0	2.9	97.1	8.8	0.1	91.1
TTF 6	Day	38.4	7.3	54.3			
	Night	24.5	25.1	50.4			
	Both	30.1	17.2	52.6	11.4	33.6	55.0
TTM 7	Day	57.8	18.3	24.0			
	Night	22.0	33.6	44.4			
	Both	40.4	26.4	33.2	11.2	40.6	48.2
TTM 10	Day	0.0	6.4	93.6			
	Night	7.4	7.1	85.4			
	Both	3.5	6.8	89.7	4.9	21.8	73.3

Values show the percentage of time spent in each habitat. Availability is given as the percentage of each habitat type found in the 99% kernel home range. Day locations include locations taken between 9:00 and 17:00, night locations were taken between 18:00 and 4:00. PS: palm swamp, FP: floodplain, TF: *terra firme*

Activity Patterns

Activity patterns show that tapirs rest during the day and begin their activity after sunset around 18:00 (Figure 19). There is an activity peak between 19:00 and 20:00 and a second peak between 3:00 and 4:00. The main foraging time seems to be between 21:00 and 3:00. These patterns were very consistent for all individuals in this study. Only TTF 5 had a somewhat higher percentage of active locations during the day (up to 30%).

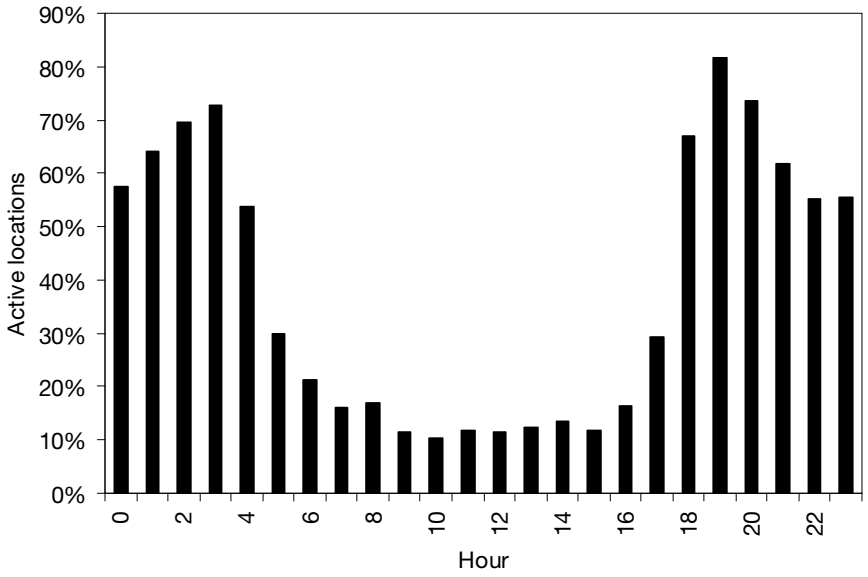

Figure 19: Average activity pattern of five individual tapirs calculated from GPS collar locations. The total number of locations was 20510. A location was classified as inactive if it was within a series of locations the animal spend at least two hours inside an areas with a radius of 100 m.

Use of Mineral Licks

Tapirs will walk over 10 km to visit a mineral lick and licks attract individuals from a large area. Tapirs usually walk to the lick and back in a single night but can spend several hours in the area surrounding a lick. They may use different licks that occur in the same general area during different nights but usually only visit one lick per night. Frequency of lick visits is irregular and time between visits can vary from only one day to over 36 days (Table 23). TTF 1 visited licks with a much higher frequency in 2005 than in 2006. Both TTF 1 and TTM 10 used established trails to move between their home range and the licks. TTF 1 was using exactly the same trail in 2005 and 14 months later in 2006.

Table 23: Data on the use of mineral licks by six radio-collared tapirs.

			Visits (N and days between visits)				
Animal	Distance (km)	Days	N	Min	Max	Average	Licks
TTF 1 A	3.2	182	29	1	18	6	2
TTF 1 B	3.2	102	8	4	36	14	2
TTF 3	10.3	7	0	-	-	-	1
TTF 5	9.4	26	0	-	-	-	1
TTF 6	0.6	22	0	-	-	-	1
TTM 7	0.4	24	3	3	14	-	3
TTM 10	2.8	58	4	3	31	-	2

Distance of the home range from the lick, number of days data was recorded, number of visits, time between visits and number of different licks visited.

Discussion

Home Ranges and Habitat Use

Despite the short duration of the majority of the datasets presented here, the data reveal an abundance of information on the movement patterns of tapirs in an Amazonian lowland forest. Home range sizes ranged from approximately 100 ha to 400 ha with an average size of 260 ha. Kernel and MCP estimates are similar at the 95% level, the large difference for TTM 10 results from the inclusion of areas outside the main range in the kernel home range, which were excluded for the MCP estimate. Due to the short duration of many of the datasets, home range size is likely underestimated for some of the individuals, and true ranges could be between 200 and 500 ha. This is comparable to data from the Bolivian Chaco where home range size for five individuals ranged from 190 to 302 ha (mean: 248 ha) (Ayala 2003), but is significantly smaller compared to data from the Atlantic forest in Brazil where home ranges in mature forest are between 119 and 1358 ha (mean 440 ha), and in secondary forest between 323 and 1085 ha (mean 645 ha) (P. Medici pers. com.). Home ranges of *Tapirus bairdii* in a lowland forest in Costa Rica on the other hand were much smaller, ranging from 59 to 194 ha (mean 107 ha) (Foerster *et al.* 2001), and two tapirs monitored in the dry forest of Santa Rosa, Costa Rica, had nightly ranges of 161 and 180 ha respectively (Williams 1984).

The kernel estimator worked well to reveal the internal structure of the home range. The separate analyses of daytime and nighttime locations showed important additional information that would otherwise have been missed, because areas of high use during the night and low use during the day (or vice versa) would have canceled each other out. Tapirs have multiple centers of activity and resting areas that often differed from feeding areas. They have a few resting places frequently visited over several weeks and they showed preferred feeding areas. Similar home range structures with differences between day and nighttime locations and multiple centers of activity were found for *T. bairdii* in Costa Rica (Williams 1984; Villalobos *et al.* 2001).

The data from TTF 1 shows that home range boundaries are very well-defined and stable over long periods of time (14 months in this case). While the animal expanded its range on one side and started using the added area extensively, the remaining boundaries did not change. On the other hand, the internal structure did change during that time. Longer datasets would be needed to evaluate the possibility that these changes follow seasonal patterns.

Since this study was designed to evaluate the use of mineral licks by tapirs, all tapirs were collared at the same lick but did not necessarily come from the same general area. Therefore the data is not suited to evaluate interactions between individuals, nor to estimate home range overlap. Data from TTF 3 and TTM 7 show that the home ranges of a male and female can overlap by almost 100 percent. According to some preliminary genetic analysis these two animals are probably siblings, so it is possible that they share their parents' territory. Foerster and Vaughan (2002) showed that a male and female pair may maintain an exclusive territory over a long time, and which they will share with their offspring for a few years. Ayala (2003) found overlaps of 80% between an adult male and a juvenile male and a 30% overlap between the same juvenile male and an adult female.

Tapirs walked an average about 5 km per night. While some of this movement is related to foraging, movement tracks showed that several individuals regularly walked along the borders of their ranges or into areas they did not use much for foraging or resting. It is

possible that the tapir are defining their territory against other individuals by maintaining clear home range boundaries.

Habitat use showed no clear patterns. Some individuals had their home range almost exclusively in *terra firme* forest while others used palm swamps, *terra firme* and floodplain forest. TTF 6 and TTM 7 share a large amount of their home range but use different habitats in different proportions. TTM 7 spends more time in the palm swamp and TTF 6 spends more time in the *terra firme* forest. Both spend more time in the palm swamp during the day than during the night. Palm swamps seem to have a certain importance for tapirs. TTF 1 expanded its range into a palm swamp and TTM 10 regularly leaves its range to visit a swamp about 3 km outside its normal range. The fruits of the palm *Mauritia flexuosa* are extensively consumed by tapirs and seems to play an important role in their diet (Bodmer 1990a; Fragoso and Huffman 2000; Chapter VI). Palm swamps also harbor a high abundance of herbaceous plants that could provide tapirs with high quality browse. It is possible that the much smaller home range sizes for TTF 6 and TTM 7 are related to a higher abundance of resources within the palm swamp. But these results show that tapirs can also live in *terra firme* forests far away from wetlands or larger rivers. This indicates that they are common throughout *terra firme* forests, which make up the largest portion of forests in the Southwestern Amazon.

Since different forest types in the Amazon usually occur in large, continuous areas, most tapir home ranges will be located in a single forest type. Tapirs might not be able to select one forest type over the other but establish their range in available areas. Habitat selection most likely occurs at the scale of a few hectares within their range, where tapirs select fruit patches or areas with abundant browse for feeding and other places for resting.

Activity Patterns

The mean activity patterns of five study animals based on the GPS data matched the patterns observed with camera traps in the study area (Chapter III), indicating that both methods are suited for evaluating activity patterns. All animals showed peaks of activity

after dawn and in the early morning. These peaks are caused by the animal moving between resting and foraging areas. During foraging, movement is reduced which results in a decline of activity. Tapirs rest at one site during most of the day but occasional movement can occur. Similar patterns were observed in the Bolivian Chaco (Ayala 2003; Noss *et al.* 2003) and for *Tapirus bairdii* in Costa Rica (Williams 1984; Foerster and Vaughan 2002). Foerster and Vaughan (2002) suggested that the nocturnal behavior of tapirs helps in thermoregulation, with tapirs resting during the hot daytime and moving around during the cooler night.

Use of Mineral Licks

The data shows that tapirs will walk 10 km and possibly further to visit mineral licks. Because all licks in the study area are located in the floodplain forest, tapirs inhabiting large areas of *terra firme* forests will have to walk long distances to visit those licks. A study from Bolivia found that two tapirs walked 6 km and 9 km to visit a lick (Herrera *et al.* 1999). The frequency of visits is irregular; tapirs can visit licks every few days for some time and then not visit them for up to 40 days. Similar irregular patterns were recorded through direct observation by Montenegro (1998) at a lick in southern Peru, but so far it is unclear what causes these irregular patterns. Tapirs can visit different licks but generally seem to visit licks in the same general area. The two individuals for which we observed multiple visits always used exactly the same trail to go to the lick and back. TTF 1 used the same trail during 14 months. Many of these tapir trails converge around licks and are clearly visible in the forest. On several occasions, TTF 1 was observed visiting a lick together with a male tapir. More data will be needed to see if visit frequency shows seasonal patterns or is related to reproductive states in females.

Conclusions and Conservation Implications

In the Amazon, tapirs are often associated with rivers, wet areas and swamps (Bodmer 1991a; Emmons and Feer 1997). This study shows that tapirs can have their home ranges entirely in *terra firme* forest far away from rivers, swamps or floodplains, suggesting that there are large populations of tapirs throughout the *terra firme* forest in southeastern

Peru. This is supported by data from camera traps from the same area, which showed no differences in relative abundance of tapirs between *terra firme* and floodplain forests (Chapter III). The data also show that palm swamps are used extensively when available to tapirs and that they might even attract individuals from nearby *terra firme* forest for sporadic visits (e.g. TTM 10). More data would be needed to show if palm swamps increase local tapir abundance and carrying capacity. The same question remains for mineral licks. While this study and others show that licks are important in many ecoregions (Montenegro 1998; Ayala 2002; Montenegro 2004; Pfeifer Coelho 2006), how tapirs meet their mineral requirements in areas where no natural licks exist nor if the availability of licks has an impact on tapir density.

Mineral licks play a special role for tapir conservation in the western Amazon. Licks are often the preferred sites for hunting tapirs and hunters can kill several individuals in a period of a few nights (Montenegro 2004; M. Tobler pers. obs.). According to the data presented, tapirs will walk 10 km and possibly more to visit a lick. This means that the area of influence of a lick can be several hundred square kilometers and a single lick can possibly be visited by dozens of tapirs. Hunters therefore can hunt at a single lick over a long period of time without noticing a significant decline in tapir abundance. However, by doing so, they can reduce the whole tapir population in a large area around the lick. The impact of a few hunters at a mineral lick can be much larger than that of hunters hunting on trails around a village. It is therefore extremely important to include mineral licks in the planning of protected areas and in management plans for local wildlife populations.

CHAPTER VII
CONCLUSIONS

Camera Traps

The results of this study showed that camera traps are a very versatile tool for studying terrestrial rainforest mammals. Camera traps are relatively simple and cheap to use and studies can be conducted over periods from a few weeks to several months depending on the objectives. The most basic use of camera traps is for species inventories. Species inventories have relatively few requirements as far as the design of the study is concerned. It is important to place cameras in all habitat types of interest and to allow for a sufficiently long survey time to record the species of interest. While common species can be recorded within a few days, the results from this study show that a large survey effort is sometimes required to achieve a fairly complete inventory. Species accumulation curves and non-parametric species richness estimators are useful tools for evaluating the completeness of an inventory.

Camera traps can also be used to study various aspects of the ecology of large and medium-sized mammals. They work especially well for species that are relatively abundant where a large number of photos can be obtained. For extremely rare species camera traps often will only be able to confirm their presence in the study area, but the amount of data won't be sufficient to look at activity patterns or habitat use.

Camera traps are the most efficient tool for studying activity patterns of many species. They don't require the handling of animals and cause much less disturbance than direct observations. They also have the advantage that they allow studies of activity patterns at a population level where data come from many different individuals, whereas telemetry studies often collect data from only a few individuals. Camera traps also allow the collection of data for several species simultaneously which allows for comparisons among species.

Camera traps are ideal for studying the use of resources of small extent such as mineral licks, water holes, nest sites or dens. One or two cameras are often sufficient to monitor the whole site and record all species visiting. This requires little effort and allows monitoring sites over long periods of time.

While many researchers currently are using camera traps to study mammals, there is still a lack of standardized methods for analyzing camera trap data. Protocols exist for capture-recapture data collected with camera traps (Karanth and Nichols 1998), but habitat use is still evaluated in many different ways (e.g. Fedriani *et al.* 2000; Moruzzi *et al.* 2002; Augustine 2004; Jacomo *et al.* 2004; Di Bitetti *et al.* 2006). Most studies used the number of photos or a related measure as an index and do not address the issue of detectability. Only recently have occupancy models been applied to camera trap data (MacKenzie *et al.* 2005; Linkie *et al.* 2007). Using occupancy models the influence of habitat and other covariates on occupancy or use of a an areas can be evaluated, incorporating detectability into the model (MacKenzie *et al.* 2006). This information could then be used for habitat viability models. Multi-season models (MacKenzie *et al.* 2003) could be used to monitor populations over time. I believe that these models will gain in popularity for the analysis of camera trap data and that further developments in occupancy models will increase the accuracy of the models and the questions that can be answered.

GPS Collars

With new, emerging GPS receivers the use of GPS collars in tropical forest has started to become feasible. Also, with the launch of new GPS satellites over the next years, better and stronger signals will become available, which will drastically increase the ability of receivers to track signals in dense forests as well as reduce position errors (Shaw 2004). While accuracy and success rates currently are lower inside the forest than outside, GPS collars can still collect much many data than would be possible with radio telemetry. This will allow researchers to collect detailed data on species where currently very little information exists. One of the main drawbacks of GPS collars is the high price. Prices

for GPS collars are still in the thousands of US dollars. However, I believe that they can reduce overall costs of a project in the long run by reducing airplane time, labor and other field expenses needed. Besides, GPS collars can usually be refurbished and can therefore be used for several seasons.

In contrast to radio telemetry data, GPS collars record continuous movement trajectories for the whole study period. These trajectories allow researchers to study not only the general home range use but also behavior such as long-distance movements, rest site choice, activity patterns and movement rates. As with camera trap data, there is a lack of methods for analyzing GPS data collected with a high temporal resolution. Most studies use methods that were developed for radio telemetry data which are usually collected at much lower intervals. For most analyses (e.g. kernel home ranges, home range overlap) the temporal order of the location is ignored. Recent methods such as the Brownian bridge movement model (Horne *et al.* 2007a), first-passage time (Fauchald and Tveraa 2003) and state-space models (Jonsen *et al.* 2003) incorporate time into the analysis and show promising results.

The Ecology of the Lowland Tapir

Lowland tapirs are common throughout the study area and use all forest types. No clear habitat preference could be detected based on camera trap and telemetry data, indicating that tapirs are habitat generalists using all forest habitats. While *Mauritia flexuosa* palm swamps are used frequently when available and *M. flexuosa* was the most common fruit found in tapir diet, the real importance of *M. flexuosa* for tapirs could only be evaluated in comparative studies including sites where the species does not exist. Interestingly, home range size and density does not seem to vary much between my study site and a site in the dry forest of the Bolivian Chaco (Ayala 2003), which could indicate that *M. flexuosa* fruits are frequently used when available but are not a key resource for tapirs.

Tapirs have a broad diet consuming over 120 species of fruit. Fruit consumption is related to availability but even in the period of highest fruit availability browse still makes up the bulk of food consumed. The high diversity and low frequency of

occurrence for most fruit species indicates that tapirs don't actively search for fruit but opportunistically consume fruits they encounter while foraging on browse. The exception might be a few common species that occur in large clumps such as *M. flexuosa*.

Tapir's home ranges show a clear structure with multiple centers of activity. They have multiple feeding areas they used during the night and multiple resting areas used during the day, with little overlap between the two. Home ranges seem to be stable over time but more data will be needed to confirm this. Several individuals repeatedly walked along the edge of their range which could indicate territoriality.

Tapirs used mineral licks frequently but at irregular intervals. Tapirs with home ranges in *terra firme* forest, away from licks, walked over 10 km to visit licks showing the importance of licks for the species. They had well-defined trails they repeatedly used to visit mineral licks.

Conservation Recommendations for Tapirs

Most of the Peruvian Amazon is still covered by forest and deforestation is concentrated in areas around a few population centers (Iquitos, Pucalpa and Puerto Maldonado) and along roads (Oliveira *et al.* 2007). While protected areas are doing well, deforestation and forest disturbance outside protected areas increased in recent years (Oliveira *et al.* 2001). The construction of new roads such as the Interoceanic Highway in Madre de Dios and the creation of new forest, mining, oil and gas concession by the Peruvian government will increase pressure on the forests.

While healthy tapir populations still exist in many parts of the Peruvian Amazon, the presence of forest as suitable habitat does not necessarily mean that tapirs are doing well. Large areas of forest can look intact on satellite images but most game species can be absent because of overhunting (Redford 1992). These "empty forests" could be repopulated by tapirs if hunting was controlled.

Tapirs are classified as vulnerable under Peruvian law and capture and hunting for commercial use is prohibited since 2004 (Decreto Supremo No 034-2004-AG).

However, subsistence hunting by indigenous people and local people is still allowed under the law and currently poses the most important threat to tapirs in the Peruvian Amazon. Since sustainable hunting of tapirs is almost impossible (Brooks *et al.* 1997), hunting should generally be prohibited. Most urgently, hunting at mineral licks should be banned and mineral licks should be protected as key resources for wildlife in the western Amazon.

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APPENDIX A

Table 24: Number of captures and capture frequency (number of photos / 1000 trap nights) for all species observed during two camera trap surveys at Los Amigos.

	Species	Common Name	2005	2006	Habit
Didelphimorphia					
Didelphidae	Didelphis marsupialis	Common opossum	21 (14.6)	16 (6.8)	T
Pilosa					
Myrmecophagidae	Myrmecophaga tridactyla	Giant Anteater	-	2 (0.9)	T
	Tamandua tetradactyla	Collared anteater	1 (0.7)	3 (0.9)	T, Ar
Cingulata					
Dasypodidae	Cabassous unicinctus	Southern naked-tailed armadillo	-	-	T
	Dasypus kappleri	Great long-nosed armadillo	2 (1.4)	9 (3.8)	T
	Dasypus novemcinctus	Nine-banded long-nosed armadillo	1 (0.7)	2 (0.9)	T
	Dasypus spp.	Long-nosed armadillo	-	10 (4.3)	
	Priodontes maximus	Giant armadillo	5 (3.5)	7 (3.0)	T
Primates					
Cebidae	Saimiri boliviensis	Common Squirrel Monkey	-	1 (0.4)	Ar*
Carnivora					
Canidae	Atelocynus microtis	Short-eared dog	4 (2.8)	7 (3.0)	T
	Speothos venaticus	Bush dog	-	-	T
Procyonidae	Procyon cancrivorus	Crab-eating raccoon	-	1 (0.4)	T
	Nasua nasua	Coati	2 (1.4)	2 (0.9)	T
Mustelidae	Eira barbara	Tayra	3 (2.1)	8 (3.4)	T
	Galictis vittata	Grison	-	-	T
	Lontra longicaudis	Neotropical otter	-	-	Aq*
	Mustela african	Amazon weasel	-	-	T, Ar*
	Pteronura brasiliensis	Giant otter	-	-	Aq*
Felidae	Puma yagouarundi	Jaguarundi	1 (0.7)	1 (0.4)	T
	Leopardus pardalis	Ocelot	15 (10.4)	31 (13.2)	T
	Leopardus wiedii	Margay	2 (1.4)	13 (5.6)	T, Ar
	Panthera onca	Jaguar	14 (9.7)	37 (15.8)	T
	Puma concolor	Puma	14 (9.7)	11 (4.7)	T

T=terrestrial, Ar=arboreal, Aq=aquatic, * species not included in the analysis

Table 24: Continued.

	Species	Common Name	2005	2006	Habit
Perissodactyla					
Tapiridae	Tapirus terrestris	Lowland tapir	39 (27.1)	63 (26.9)	T
Artiodactyla					
Cervidae	Mazama americana	Red brocket deer	8 (5.6)	31 (13.2)	T
	Mazama gouazoubira	Grey brocket deer	17 (11.8)	36 (15.4)	T
Tayassuidae	Tayassu pecari	White-lipped peccary	95 (66)	115 (49.1)	T
	Pecari tajacu	Collared peccary	23 (16.0)	19 (8.1)	T
Rodentia					
Dasyproctidae	Dasyprocta punctata	Brown agouti	50 (34.7)	48 (20.5)	T
	Myoprocta acouchy	Green acouchy	2 (1.4)	15 (6.4)	T
Sciuridae	Sciurus spadiceus	Southern Amazonian red squirrel	-	5 (2,1)	Ar
Caviidae	Hydrochoerus hydrochaeris	Capybara	-	-	T, Aq*
Dinomyidae	Dinomys branickii	Pacarana	-	-	T
Cuniculidae	Cuniculus paca	Paca	14 (9.7)	33 (14.1)	T
Echimyidae	Proechimys sp.	Spiny Rat	-	9 (3.4)	T*
Lagomorpha					
Leporidae	Sylvilagus brasiliensis	Brazilian rabbit	-	3 (1.3)	T
Aves	Crypturellus undulaus yapura	Undulated tinamou	4 (2.8)	25 (10.3)	*
	Mitu tuberosa	Razor-billed curassow	28 (19.4)	26 (11.1)	*
	Penelope jacquacu	Spix's guan	7 (4.9)	6 (2.6)	*
	Psophia leucoptera	Pale-winged trumpeter	56 (38.9)	140 (59.8)	*
Terrestrial mammals			21	24	
All mammals			21	27	

APPENDIX B

Table 25: List of seed species found in 135 samples of tapir dung collected between May 2005 and October 2007 in the Peruvian Amazon.

Species	Samples	Months	Number[a]	Weight (g)	Length (mm)	Width (mm)
Anacardiaceae						
Spondias mombin	3	2	15 (1-37)	2.59	30.0	19.0
Annonaceae						
Annona sp. 1	2	1	8 (6-10)	0.21	1.9	1.2
Annona sp. 2	1	1	2 (2-2)	0.36	17.2	11.9
Duguetia riparis	14	6	3 (1-10)	0.59	18.2	8.9
Fussaea longifolia cf.	1	1	1 (1-1)	0.41	29.0	13.0
Indet Indet	3	3	9 (1-25)	0.33	17.0	10.0
Onychopetalum periquino	22	5	20 (1-104)	1.19	20.1	13.7
Oxandra xylopioides	6	3	55 (1-235)	0.67	17.0	11.0
Porcelia nitidifolia	1	1	4 (4-4)	3.95	38.2	21.4
Rollinia sp. 1	7	2	84 (2-401)	0.05	8.7	5.5
Rollinia sp. 2	2	1	247 (2-492)	0.06	8.0	6.0
Rollinia sp. 4	1	1	1 (1-1)	0.01	5.2	4.0
Apocynaceae						
Macoubea guianensis	2	2	2 (1-4)	0.23	18.1	6.7
Araceae						
Heteropsis spruceana	1	1	3 (3-3)	0.01	4.3	3.6
Arecaceae						
Astrocarium murmurum	10	6	6 (1-21)	6.39	43.3	24.3
Bactris hirta cf.	8	5	2 (1-4)	0.07	16.0	7.0
Mauritia flexuosa	62	12	0 (0-11)	5.34	26.5	21.5
Oenocarpus batua	2	2	10 (2-17)	1.16	26.0	14.0
Oenocarpus mapora	1	1	52 (52-52)	5.68	28.0	22.2
Bombacaceae						
Ceiba pentandra	1	1	1 (1-1)	0.01	5.0	2.0
Indet Indet 12	38	12	19 (1-152)	0.01	6.0	3.5
Matisia cordata	2	2	6 (3-9)	0.72	29.0	15.0
Ochroma pyrimidale	6	4	5 (1-20)	0.08	9.0	5.0
Pachira aquatica	1	1	6 (6-6)	3.19	24.0	18.0
Burseraceae						
Protium amazonicum cf.	1	1	1 (1-1)	1.12	18.0	16.0
Protium sp. 1	4	3	2 (1-2)	1.20	18.0	12.5
Protium sp. 2	2	1	2 (1-3)	0.15	10.0	10.0
Caricaceae						
Jacaratia digitata	5	4	5 (3-11)	0.02	6.0	4.0

[a] Mean and range of the number of seeds found in each sample. Number for very small seeds were extrapolated from a subsample.

Table 25: Continued.

Species	Samples	Months	Number[a]	Weight (g)	Length (mm)	Width (mm)
Cecropiaceae						
Cecropia sp. 1	3	2	366 (3-758)	0.01	1.9	1.2
Cecropia sp. 2	1	1	3 (3-3)		3.0	1.0
Cecropia sp. 3	2	2	40 (33-48)	0.01	4.0	1.3
Cecropia sp. 4	14	7	496 (2-3450)	0.01	2.5	1.2
Cecropia sp. 5	1	1	45 (45-45)	0.01	2.6	1.4
Pourouma minor	5	3	2 (1-2)	0.26	13.0	8.5
Chrysobalanaceae						
Hirtella racemosa cf.	2	1	1 (1-1)	0.02	9.0	5.3
Hirtella sp. 1	2	2	1 (1-1)	0.06	12.0	8.0
Clusiaceae						
Visma sp. 1	1	1	1 (1-1)	0.01	5.0	2.5
Clusia sp. 1	1	1	3 (3-3)		4.0	2.5
Clusia sp. 2	2	1	2 (1-2)	0.01	3.0	2.0
Cyperaceae						
Euphorbiaceae						
Indet sp. 1	1	1	1 (1-1)	0.01	5.0	3.0
Indet sp. 3	2	2	1 (1-1)	0.67	14.0	12.4
Indet sp. 2	1	1	20 (20-20)	0.13	9.2	8.1
Indet sp. 1	1	1	1 (1-1)	0.06	8.0	6.0
Scleria macrophylla	3	3	1 (1-2)	0.02	5.0	3.0
Senefeldera inclinata	2	2	8 (7-9)	0.72	14.6	13.0
Fabaceae						
Acacia sp. 1	1	1	7 (7-7)	0.04	9.0	6.0
Hymenaea oblongifolia	1	1	46 (46-46)	5.08	32.0	21.0
Indet Indet	1	1	1 (1-1)	0.04	5.0	4.5
Mimosa sp. 1	1	1	5 (5-5)	0.88	20.0	10.0
Ormosia sp. 1	2	2	1 (1-1)	0.13	8.0	7.0
Parkia pendula	1	1	1 (1-1)		11.0	5.0
Senna sp. 1	8	3	14 (1-39)	0.06	8.0	5.0
Fam Indet						
Casearia sp. 1	1	1	3 (3-3)	0.01	2.5	2.2
Casearia sp. 2	1	1	5 (5-5)	0.01	4.0	3.0
Flacourtiaceae						
Indet sp. 1	1	1	2 (2-2)		6.0	5.0
Hugoniaceae						
Hebepetalum humiriifolium	1	1	2 (2-2)	0.10	8.7	5.2
Icacinaceae						
Calatola sp.	3	2	7 (2-11)	1.58	20.0	14.0
Lecythidaceae						
Couropita guianensis	1	1	1 (1-1)	0.12	10.0	8.0

Table 25: Continued.

Species	Samples	Months	Number[a]	Weight (g)	Length (mm)	Width (mm)
Icacinaceae						
Calatola sp.	3	2	7 (2-11)	1.58	20.0	14.0
Lecythidaceae						
Couropita guianensis	1	1	1 (1-1)	0.12	10.0	8.0
Malpighiaceae						
Byrsonima sp. 1	1	1	1 (1-1)	0.14	7.0	6.0
Melastomataceae						
Miconia sp. 1	1	1	1 (1-1)	0.01	3.0	3.0
Miconia sp. 2	1	1	1 (1-1)	0.01	4.0	2.0
Miconia sp. 3	1	1	1 (1-1)	0.01	3.1	3.0
Miconia sp. 4	1	1	1 (1-1)	0.01	5.0	2.5
Menispermaceae						
Anomospermum reticulatum cf.	3	2	3 (1-6)	6.98	31.4	22.5
Moraceae						
Brosimum alicastrum	8	5	4 (1-10)	0.28	10.5	9.5
Clarisia racemosa	2	2	2 (1-3)	2.30	19.0	18.0
Ficus sp. 1	6	5	54 (1-215)	0.01	2.0	1.2
Ficus sp. 2	1	1	16200 (16200-16200)	0.01	1.5	1.3
Ficus sp. 3	3	3	3 (2-5)	0.01	3.3	1.9
Ficus sp. 4	37	11	370 (1-4888)	0.01	3.1	1.5
Ficus sp. 5	3	3	2966 (1917-3916)	0.01	3.0	1.5
Ficus sp. 6	1	1	46 (46-46)	0.01	1.5	1.1
Ficus sp. 7	13	6	1309 (19-13144)	0.01	2.8	1.1
Ficus sp. 8	2	2	1436 (15-2856)	0.01	1.2	0.7
Ficus sp. 9	4	4	33 (3-61)	0.01	1.5	1.3
Ficus sp. 10	4	3	1164 (40-2705)	0.01	2.0	1.1
Ficus sp. 11	1	1	580 (580-580)	0.01	2.0	0.9
Ficus sp. 12	5	4	614 (5-2950)	0.01	2.8	1.5
Ficus sp. 13	18	10	16252 (2-167850)	0.01	1.6	1.0
Ficus sp. 14	4	3	1569 (12-5650)	0.01	1.8	1.3
Helicostylis tomentosa	1	1	1 (1-1)	0.18	10.0	8.0
Perebea sp. 1	1	1	2 (2-2)	0.08	10.0	5.0
Perebea sp. 2	8	3	7 (2-21)	0.09	8.0	7.0
Perebea sp. 3	1	1	1 (1-1)	0.24	15.0	9.0
Perebea sp. 4	30	7	27 (1-139)	0.24	15.0	10.0
Perebea sp. 5	7	3	6 (1-15)	0.15	8.0	8.0
Myrtaceae						
Eugenia florida cf.	1	1	1 (1-1)	1.09	19.0	13.0

Table 25: Continued.

Species	Samples	Months	Number[a]	Weight (g)	Length (mm)	Width (mm)
Myrtaceae						
Olyra sp. 1	1	1	1 (1-1)	0.01	2.0	1.3
Poaceae						
Psidium sp. 1	1	1	30 (30-30)	0.01	4.0	3.0
Polygalaceae						
Moutabea aculeata	1	1	1 (1-1)	0.04	9.0	5.0
Rubiaceae						
Borojoa sp. 1	3	3	14 (4-32)	0.04	7.0	4.0
Genipa americana	23	10	57 (1-403)	0.04	6.1	4.0
Indet sp. 84	1	1	3 (3-3)	0.01	3.0	2.0
Indet sp. 57	2	1	8 (1-14)	0.01	4.0	4.0
Palicourea sp. 1	1	1	8 (8-8)	0.04	7.0	5.0
Palicourea sp. 2	2	2	1 (1-1)	0.01	4.0	4.0
Palicourea sp. 3	2	2	6 (1-12)	0.01	3.5	3.2
Palicourea sp. 4	1	1	1 (1-1)	0.01	4.0	3.0
Palicourea sp. 5	3	3	3 (2-4)	0.01	3.3	2.5
Palicourea sp. 6	2	2	2 (1-2)	0.04	6.0	5.0
Psychotria sp. 1	2	2	1 (1-1)	0.01	3.5	3.3
Psychotria sp. 2	1	1	1 (1-1)	0.06	9.0	4.0
Psychotria sp. 3	1	1	1 (1-1)	0.05	6.0	5.0
Psychotria sp. 4	1	1	1 (1-1)		5.0	4.0
Psychotria sp. 5	1	1	1 (1-1)		4.0	3.0
Psychotria Sp. 6	1	1	1 (1-1)	0.01	3.0	2.7
Psychotria sp. 7	1	1	2 (2-2)	0.01	2.0	2.0
Psychotria sp. 8	1	1	1 (1-1)	0.03	5.0	3.5
Sapindaceae cf.						
Indet sp. 1	1	1	4 (4-4)	0.02	19.1	9.5
Sapotaceae						
Pouteria putamen-ovii	2	1	2 (1-2)	2.52	33.5	19.8
Pouteria sp. 1	4	2	3 (1-4)	0.20	15.0	8.5
Pouteria sp. 2	9	2	46 (1-382)	0.37	18.3	9.7
Pouteria sp. 3	3	2	5 (1-13)	0.30	16.0	8.6
Pouteria sp. 4	9	5	4 (1-10)	0.28	16.2	9.3
Sarcaulus sp. 1	1	1	1 (1-1)	0.84	27.2	12.0
Sarcaulus sp. 2	4	3	1 (1-2)	0.39	24.3	11.0
Simaroubaceae						
Simarouba amara	2	1	1 (1-1)	0.07	10.4	6.3

Table 25: Continued.

Species	Samples	Months	Number[a]	Weight (g)	Length (mm)	Width (mm)
Solanaceae						
Cestum cf. sp. 1	1	1	2 (2-2)	0.01	6.0	3.0
Sterculiaceae						
Guazuma ulmifolia	8	3	670 (2-2080)	0.01	2.2	1.0
Violaceae						
Rinorea sp. 1	2	2	2 (1-3)	0.03	6.0	4.0
Rinorea sp. 2	1	1	1 (1-1)	0.19	11.0	8.0
Rinoreocarpus ulei	1	1	4 (4-4)	0.01	6.7	2.5

VITA

Mathias Werner Tobler received his Master of Science degree in environmental sciences from the Swiss Federal Institute of Technology Zürich (ETH Zürich). He conducted undergraduate research on Baird's tapirs in the Talamanca Mountains of Costa Rica and wrote his master's thesis on the impact of cattle ranching on a savanna ecosystem at the coast of Tanzania. In 2002 he started working with the Botanical Research Institute of Texas on a project in the Peruvian Amazon, which led to his doctoral research. He graduated with his Ph.D. at Texas A&M University in May 2008 and will continue to work on research and conservation projects in Peru.

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